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TITLE

Studies on the Biology of Ammocoetes in Streams

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INTRODUCTION

This manuscript report complements Manuscript Report No. 710, "The Distribution of Sea Lamprey Ammocoetes in the Lake off Eight Rivers Draining into the Canadian Waters of Lake Superior," issued in November 1961. Together they complete the account of ammocoete studies carried out at the Biological Station, London, from 1957 to 1962.

Although most aspects of the ecology of ammocoetes will be discussed below in the literature, research has been mainly confined to the topics of growth and length of larval life, distribution within populations and migration.

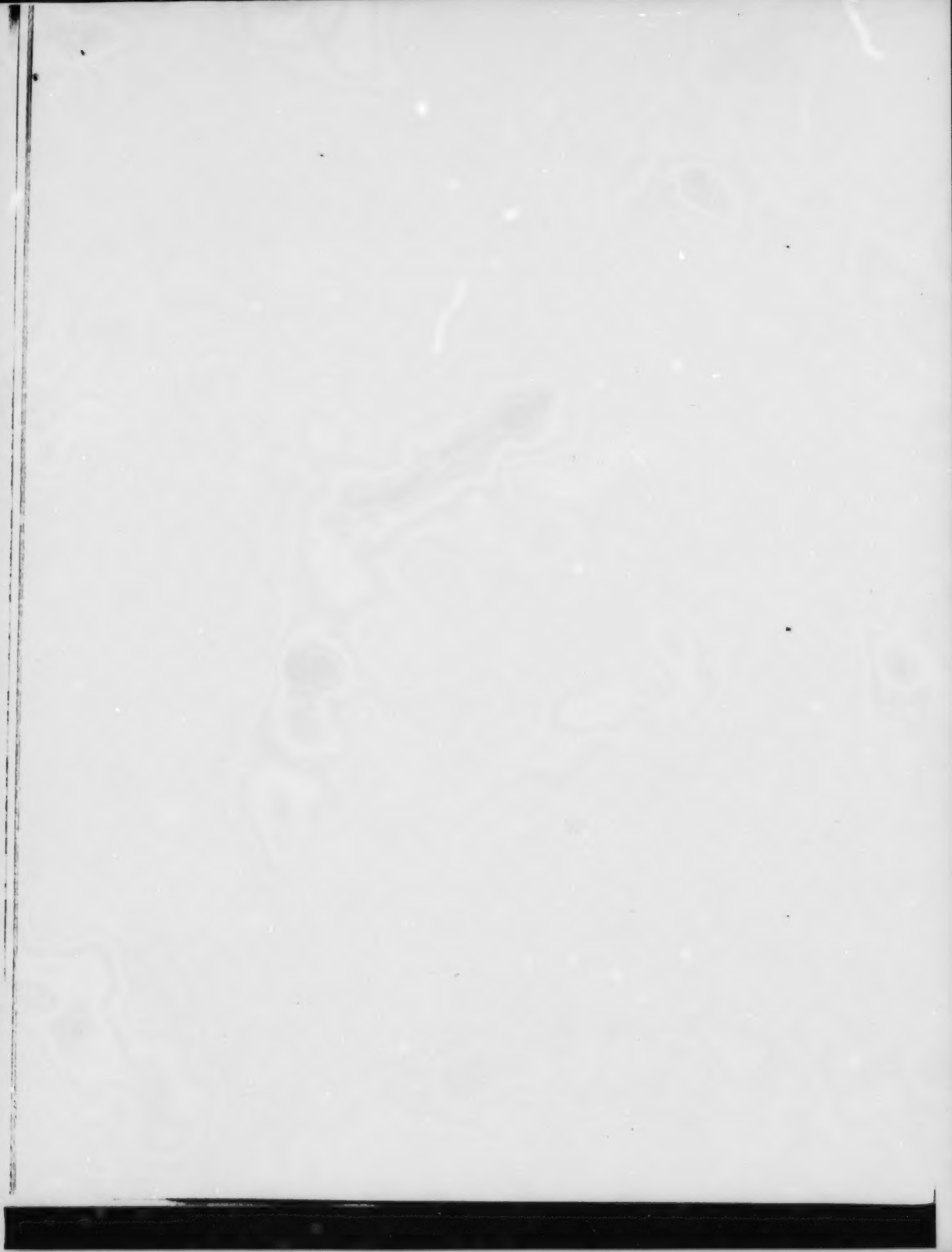
Lampreys, because of their peculiar structure and phylogenetic position, have long attracted the attention of zoologists. However, most research has been directed at adult lampreys and little of it has been ecological in nature. Comparatively little work has been carried out on the ammocoete larva of lamprey; indeed, it was not until 1856 that the identity of this animal as a larval lamprey was established (Muller, 1856).

Interest in lampreys has increased in recent years, largely because of the problems associated with the spread of the sea lamprey, Petromyzon marinus L., through the Great Lakes above Niagara Falls and the consequential decline of their commercial fisheries (Applegate, 1950; Dymond, 1922; Eschmeyer, 1957; Hile, 1949; Hile, Eschmeyer and Lungert, 1951; Shetter, 1949). Control of sea lamprey populations in the Great Lakes is being attempted. Early methods of attempted control utilized mechanical and electrical weirs to capture or kill the vulnerable spawning migration into the rivers each spring (Applegate, Smith and Nielsen, 1952; MacKay and MacGillivray, 1949; Shetter, 1949). Recently control using a selective larvicide to kill larvae in streams was started (Applegate, Hall, Howell and Smith, 1957). This method of control increased the need for knowledge of ammocoete ecology and in consequence several projects, including the one described herein, were carried out under the Great Lakes Fishery Commission to provide more information.

Four species of lampreys have been found in Ontario. These are: Ichthyomyzon unicuspis Hubbs and Trautman, the silver lamprey; I. fossor Reighard and Cummins, the Michigan brook lamprey; Entosphenus (Lampetra) lamottei (Le Sueur), the American brook lamprey; and Petromyzon marinus L., the sea lamprey (Slashtenenko, 1958; Scott, 1954). Only the latter two species will be considered in detail in this report, although brief mention is made of the others where sufficient data was collected.

LITERATURE REVIEW

Few studies of the ecology of ammocoetes were conducted prior to about 1930, and even at the present time knowledge of the biology of these animals is sparse and patchy. There are several reasons for this condition. Lampreys in the ammocoete stage spend all but a small portion of time in a



fossorial existence. Thus, lamprey larvae are often not noticed even where they are abundant. In addition, they are hard to capture. Before the advent of electro-shocking techniques for fish capture, digging ammocoetes out or draining the stream were the only methods of collecting the animals. Yet another difficulty lies in the identification of ammocoetes, once captured. For many species this is still impossible, and even where keys are available the task is by no means straightforward. A further difficulty is encountered if ammocoetes are to be kept in a laboratory for experimental purposes. In captivity ammocoetes must be provided with a soft substrate into which they can burrow; deprived of this, life is short and mucus often blocks the gills, quickly causing death. Given suitable substratum and temperatures within their tolerance, ammocoetes may be kept for long periods. Feeding is, however, a problem unless a natural source of water rich in diatoms is available. Unfed ammocoetes may live long periods, but shrink in size and finally die. It is not surprising, therefore, that ammocoete ecology has been neglected.

It is doubtful that lamprey larvae were even recognized as such prior to 1856; when Müller (1856) showed their true identity. Prior to that date, ammocoetes had been called a separate species, Ammocoetes branchialis Cuvier. It is possible, however, that the identity of ammocoetes as lamprey was realized before Müller's paper. In early writings it is usually impossible to discern whether some descriptions refer to larvae or to newly transformed lampreys. Elyote (1559) describes "lumbrici" as smaller than lampurnes (Lampetra fluviatilis) and somewhat yellowish in colour. This may well have referred to ammocoetes. Similarly, Pennant's (1776) description of "pride" usually taken to be Lampetra planeri, which he describes as "lodging themselves in the mud, and are never observed to adhere to anything like other lamprey," certainly may describe ammocoetes. However, the fact remains that little was written of the habits of ammocoetes before Müller's (1856) account. A paper by Gage (1893) is a notable work that covers many details of lamprey biology.

a) Ammocoete Distribution within Streams

Gage (1893) noted that ammocoetes made their burrows in sand and mud, and that suitable locations were often found in concavities of the stream bed. Reighard and Cummins (1916), in reporting studies on the habits of the Michigan brook lamprey, Ichthyomyzon fossor, observed that ammocoetes were most abundant where eddies had deposited silt in the concavities of the stream bed, where the current was slow. They considered that a mixture of silt and sand provided the most favourable habitat, but noted that ammocoetes were also present in gravelly and pure sand bottoms. Léger (1920) recorded that larvae of Petromyzon marinus lived in burrows in mud and fine sand. Schultz (1930) conducted a thorough study of Lampetra planeri in the State of Washington, U.S.A. His observations essentially confirmed that ammocoetes of that species had similar habits to those described for I. fossor by Reighard and Cummins. He found ammocoetes to be most abundant in eddies where a rich deposit of silt mixed with a little sand had settled; ammocoetes were also common where concavities of the stream bed had allowed the general drift of debris and silt to settle. Very few

were present in shifting sand bottoms, and they were not abundant in firm silt where plants were established. Enequist (1937) stated a belief that ammocoetes were attracted to rotting vegetation. Leach (1940), in discussing the distribution of I. fossor in streams, expressed the belief that the nature of the streams affected distribution. He believed that in rivers of fairly constant flow and consequently stable bottoms, ammocoetes segregated by size in various deposits. In streams of more variable flow, however, where deposits were more mixed and less stable in nature, the segregation was less marked. Hardisty (1944) investigated the distribution of L. planeri in England. He found that ammocoetes were generally distributed in streams, except in very small ones. They were found only where the current was sluggish or where the stream meandered. Ammocoetes were most abundant in eddies and backwaters, below obstructions such as fallen trees or on bends in the stream. The type of mud inhabited varied, but larvae were most numerous in fine silt containing decaying organic matter. They sometimes occurred in silt-sand mixtures but seldom in coarse sand or gravel. Like Schultz (1930), Hardisty noted that ammocoetes were most numerous toward the water line. Maskell (1929), in his thorough work on the New Zealand lamprey, Geotria australis, showed that this species had similar habits to those of European lamprey. He found ammocoetes to be most numerous in mixtures of fine mud and sand, but absent in stiff clay and only the larger specimens were present in gravel. Areas of suitable habitat for ammocoetes were found along the river banks and in small backwaters; frequently these spots were covered with either sunken or floating fallen leaves, twigs, and other debris. Like Leach (1940), Hardisty found that ammocoetes were segregated by size in different deposits. Small animals were found in fine silt, while longer ones occurred where there was a deep layer of decaying debris. The largest ammocoetes were found among debris containing little or no mud. Metamorphosing individuals were sometimes found in pure sand and even gravel. Churchill (1947), also working on I. fossor, stated that ammocoetes require a fairly soft bottom in which to burrow. He noted their absence in firm sand and, curiously, in extremely soft mud. Like many of the aforementioned authors, he considered the best substrate to be a mixture of sand and silt. He considered that a depth of water of 6 to 24 inches with aquatic vegetation was most suitable. Ammocoetes were found, however, in water as deep as 3 feet. The most complete account published to date on ammocoete ecology, and indeed on most phases of sea lamprey biology, is that of Applegate (1950). This account is concerned with the biology of landlocked P. marinus. Ammocoete work was carried out in the Ocqueoc River, Michigan, U.S.A. Applegate found that the most important parameter controlling ammocoete distribution was the softness of the bottom. Ammocoetes were most abundant in soft bottoms of silt, silt-sand, silt-debris, etc. These deposits were normally present where the current was slack, for example, in eddies, backwaters and on the inside of stream bends. Ammocoetes were found in suitable bottoms to a depth of 7½ feet of water. Where springs and seepage into the bottom occurred, ammocoetes were rare. In contrast to Schultz (1930) and in common with Churchill (1947), Applegate found ammocoetes abundant where aquatic vegetation was established in small patches. Like Hardisty (1944) and Leach (1940), Applegate found some segregation by size. Young-of-the-year first occupied sites with mixtures of fine sand and silt, but by the end of their first year had moved to more "mucky"

bottoms. In shifting and unstable sand bottoms ammocoetes were much less abundant than in stable silted sites. As an example, a sand bottom adjacent to a silted slough had an average of one ammocoete over one year old per square foot, whereas in the slough three per square foot was the mean population density. Areas of fine compacted sand, and gravel, were found to harbour few ammocoetes. Wigley (1959), also working on landlocked P. marinus, added nothing to Applegate's account of ammocoete habits. Baxter (1957), a British worker, made some broad generalizations concerning ammocoete habitats. He observed that the "beds" occupied by ammocoetes were stable in nature and that the ammocoetes lived in them for long periods. He postulated that such beds, and thus ammocoete populations, were most likely to occur where the stream gradient was between 10 and 30 feet per mile. Schroll (1959) added some new information concerning ammocoete habitats. He found that L. planeri and L. danfordi were found in heavily shaded brooks and in slow river reaches. He found that larvae sought out a depth of mud proportional to their age and size. He also noted that small ammocoetes built burrows in substrate with finer particles than did large ammocoetes, and that the bottom in which large ammocoetes built burrows was less homogeneous in regard to particle size than that in which small ammocoetes built their burrows. He stated that the water flow over ammocoete burrow locations was constant, with a surface velocity of 2.07 feet per second.

Table I summarizes data given by the various authors on bottom types inhabited by ammocoetes and their relative abundance or noted absence.

b) Migration in Ammocoetes

Since the migration of ammocoetes and their broad distribution in streams are functions of the same process, these are considered as one topic.

It has long been realized that ammocoetes are present below lamprey-spawning sites and rare or absent above, a fact indicating downstream migration. Lamprey larvae leave the nest soon after hatching (Gage, 1893; Applegate, 1950). Applegate (1950) showed that at an average water temperature of 71°F, larval P. marinus left the nest 18 to 21 days after the eggs were laid; most ammocoetes left on the 20th day. This exodus from the nest is believed to be a voluntary action (Gage, 1893; Applegate, 1950). After ammocoetes take up their abode in suitable substratum below the spawning sites, the amount of migration appears to vary according to flow characteristics of the streams. Schultz (1930), in discussing L. planeri, believed that the bulk of migration in the streams which he studied occurred soon after hatching, as the smallest larvae were widely distributed within a few months of hatching. He attributed the relatively stable condition of the population to the fact that the streams had a nearly constant flow. Leach (1940) made similar observations of populations of L. fossor in an Indiana stream; in that stream, too, flow was relatively constant. Leach (1940) also remarks that, from his experience in digging ammocoetes in many other localities, he believed that the broad distribution was governed by flow characteristics and bottom types. Baxter (1957), in a general review of

distribution of British lampreys within streams, considered that ammocoetes remained in stable ammocoete beds that could withstand wide flow changes for long periods, and did not move downstream. Hardisty (1944), in investigations of *L. planeri* in Britain, found that samples of larvae from higher reaches of streams contained a smaller number of larger larvae than samples from further downstream. He wrote: "It is probable that there is a gradual movement of ammocoetes downstream, resulting in a higher proportion of older larvae in the lower reaches, but this is almost certainly a passive migration during periods of flooding." Enequist (1937), writing of *L. fluviatilis* and *L. planeri* (which he considers as a single species) in Sweden, reported that he found, in one river, ammocoetes mainly of a size range of 20-30 millimeters close to the spawning site, 40 kilometers (24.8 miles) from the mouth. Five kilometers (3.1 miles) from the mouth of the same river ammocoetes captured were all 80-130 millimeters in length. Enequist believed that a certain critical water velocity was essential for migration, which he considered a passive process. In rivers of a slow meandering nature; where this velocity was not exceeded, little migration could be expected. In rivers, where flow exceeded this velocity, concentrations of ammocoetes would occur in ponds, dams, or at the mouth of the river. Thus ammocoetes reached at least brackish water in rivers emptying into the sea, and no doubt were present in lakes in the courses of other streams. In general, evidence points to the fact that all migration is downstream. Churchill (1947), in his survey of the Brule River, Wisconsin, U.S.A. for ammocoetes of *L. fossor*, found no ammocoetes above the riffle where spawning took place. Applegate (1950), in a similar survey of the Ocqueoc River, Michigan, U.S.A. for sea lamprey larvae, found none above the highest point of spawning. Stauffer and Hansen (1958a) studied migration in *P. marinus* larvae using a variety of methods. Short distance upstream migration was indicated by the occasional discovery of lamprey larvae at the mouths of streams which lacked spawning facilities. By clearing certain areas of ammocoetes with an electric shocker and later re-checking these areas, evidence of extensive migration was obtained. By marking ammocoetes and returning them to a stream at two points, one above and one below a test area, and then making collections from the test area, it was shown that migration was entirely downstream. Further evidence of a lack of upstream migration was obtained using a weir above all ammocoete populations in another stream. No ammocoetes were caught in the weir. Abundant evidence of the downstream migration of large numbers of sea lamprey ammocoetes was obtained by Applegate (1961) from the operation of an inclined screen (Wolf trap near the mouth of the Carp Lake River, Michigan, U.S.A., from 1948 to 1958). The mean annual catch of larvae in the trap from 1950-51 to 1956-57 was approximately 9000 specimens. It was found that most ammocoetes moved down during flood conditions, the greatest activity being in March, April and May during the spring "breakup". The least amount of migration took place in August and September. Most ammocoetes caught were approximately 127 millimeters in length, but the size range from 49 to 177 millimeters showed that some larvae of all size groups but the very smallest migrated at that location. The position of the trap was only 1500 feet from the mouth of the stream at Lake Michigan; this suggested that under normal circumstances the migration would continue out into the open lake. Applegate (1950) had shown that ammocoetes were present right at the

mouth of the Ocqueoc River, Michigan, a fact also suggestive of ammocoete presence in the lake. Stauffer and Hansen (1958a) demonstrated the presence of small numbers of P. marinus, E. (L.) lamottei and Ichthyomyzon spp. in Lake Michigan up to 1¼ miles from the parent stream and in depths down to 15 feet.

c) Free-swimming Activity in Ammocoetes

Very few observations have been made of natural free-swimming activity of larval lampreys. Enequist (1937), believing such free-swimming activity must take place sometimes, was able to observe it in a Swedish river at night. Wading in 20-centimeter deep water at night, he observed larval lampreys swimming in a haphazard way at the water surface. Illuminated by a flashlight, these animals immediately dived and burrowed into the bottom. Enequist also noticed that those free-swimming ammocoetes that were in contact with the bottom orientated themselves so that they swam against the current. Most other observations on free-swimming ammocoetes have been made in daylight when the animals have been induced to leave the bottom in some way. Gribble (1939) observed such free-swimming activity in a stream which dried to small pools. In these pools ammocoetes remained free swimming for three weeks. Applegate (1950) made some observations on the swimming behaviour of sea lamprey ammocoetes disturbed by electric shocker. He observed that those allowed to drift downstream swam aimlessly with the current until sluggish or slack water was reached, where they dived to the bottom and burrowed. He observed also that young-of-the-year ammocoetes released in aquaria dived immediately for the bottom and buried themselves if it were suitable.

d) Burrowing and Behaviour in the Burrow

One aspect of ammocoete behaviour, namely, that of leaving its burrow when the surface of the bottom is exposed to the air, has often led to their discovery and has provided a method for their capture. This has been exploited in the usual method of ammocoete collection, wherein mud is shovelled on to the bank and the ammocoetes caught as they wriggle free. One of the earlier lamprey papers, that of Gage (1893), is the most thorough account of ammocoete behaviour so far published. This important work has been overlooked by many subsequent authors, who have repeated Gage's observations and experiments. Gage observed ammocoetes both burrowing and in their burrows in glass containers. Ammocoetes released in these containers over a suitable substratum immediately started to bury themselves. The process was observed to consist of two stages. In the first stage, the ammocoete standing vertically on its head made vigorous swimming movements, at the same time twisting the oral hood from side to side; this process continued until the branchial basket was buried. At this point the ammocoete ceased to push itself into the sand by swimming movements and used a second method involving only the buried portion. The sand was parted ahead of the larva by the stiff oral hood. During this stage of burrowing the ammocoete moved in such a way as to form a U-shaped burrow, usually with an opening at the head end. In the burrow the larva remained constantly with the dorsal surface up, and was able to move easily inside

the burrow. The sand lining the burrow was compacted and did not cave in. Gage noted that the ammocoetes were able to make new burrows with new openings from within the sand. Larvae, when disturbed, would leave an established burrow and worm their way rapidly through the sand. Gage was of the opinion that an ammocoete would not leave the sand if it could possibly avoid it.

Gage (1893) also made several important observations concerning the response of lamprey larvae to light. It was known that ammocoetes avoided light, and Parker (1905) investigated this response in some detail. He found that the tail was the light-sensitive region. Young (1935) added to this work with experiments on the light sensitivity of the whole body. Young confirmed that the tail was most sensitive to light, but that illumination of the spinal cord or head would also elicit responses. Young demonstrated that this response was not a true taxis, but that light stimulated swimming activity; the response could therefore be described as photokinesis. It was observed that swimming movements included preliminary burrowing movements, the burrowing being particularly strong when the animal swam from darkness into light. Young suggests that the photosensitivity of the tail is important in behaviour, in that it ensures that ammocoetes bury themselves completely. Gage (1893) tested the reactions of buried ammocoetes to light; he found that buried larvae did not tend to move away from light. It would seem therefore that illumination may serve as a stimulus to swimming and burrowing in exposed ammocoetes, but that once buried there is no reaction to light. Gage's (1893) account referred to larvae of P. marinus and E. (L.) lamottei. Reighard and Cummins (1916) reported similar behaviour in L. unicuspis, and Schultz (1930) found no difference from this in L. planeri.

Applegate (1950) added to the available information on ammocoete burrows. He found that the depth of burrow was proportional to the larva's size. Table II summarizes this information. Applegate also noticed that shallower burrows were constructed in sand than in heavy black muck. In a stratified bottom, with muck overlying sand, burrows were constructed entirely in the muck. Applegate described the burrows as ill-defined; he observed ammocoetes coming to the surface while feeding, but retreating to the bottom of the burrow when disturbed and at irregular intervals. Lanzing (1957) states that the head of the larva extends from the burrow during feeding, and other authors also make this statement. However, such behaviour is contrary to the observations of many authors (Gage, 1893; Reighard and Cummins, 1916; Applegate, 1950). Leach (1940) records some observations which may explain this contradiction. Describing the behaviour of L. fossor, he noted that while ammocoetes were never exposed, transforming specimens often lay with the entire pharynx out of the sand.

Sawyer (1959) added to the knowledge of the burrowing process. He found that ammocoetes would burrow into a wad of cotton and could be observed while doing so. The oral hood was observed to be the main digging organ; it displayed great mobility. While the body was held rigidly in the sand by muscular waves, the head was pushed forward with the oral hood contracted to a point, which constantly moved from side to side seeking the best path. When pushed forward as far as possible, the hood was flared out

and served as an anchor while the body was pulled up. This process was then repeated. A similar method of digging is well known in many bivalve molluscs.

Schroll (1959) found that the depth of ammocoete burrows increased with their age in quite a regular manner.

e) Food and Feeding in Ammocoetes

Food and feeding in ammocoetes has received more attention than many other aspects of their biology. However, in the early literature only generalized statements are made, for instance, Gage (1893) merely stated that the food of the larvae consisted of microscopic organisms. Léger (1920), studying P. marinus, noted that the larvae ate mainly microscopic algae and that those eaten were principally diatoms. He noted that some protozoa, notably "Arcelles", were eaten. The first exhaustive study of the subject was carried out by Creaser and Hann (1929), who investigated the food of a species they called Entosphenus appendix DeKay which is now called E. (L.) lamottei. These authors concluded that diatoms and desmids were the main food; protozoa were also found in the intestinal contents, but their contribution was difficult to assess because of rapid digestion of these forms. All intestines examined contained sand crystals. All the organisms present in the ammocoete intestines were also found in surface water, but were much more common in the layer of sediment and detritus on the surface of the bottom. They concluded that none of the food came from the stream bed itself. Sawyer (1957) fed ammocoetes on green water cultures. Schroll (1959) has recently published results complementary to those of Creaser and Hann (1929), but concerned with two different species, L. planeri and L. danfordi. Working in Europe, he examined intestinal contents and stream flora at all seasons of the year, and also carried out feeding experiments in the laboratory. Schroll found that when diatoms were available, these constituted the main source of food; at other times more detritus was consumed. In the stream and in ammocoete intestines diatoms were most common in the summer. In laboratory experiments, diatoms, marl and activated charcoal were actively ingested. Starch, wheat flour, etc. were ingested less actively. Paramoecium, finely chopped tubificids and fish food were taken into the branchial basket, but did not appear in the intestine; paramoecia often were harmful and damaged or killed the ammocoetes.

The method of feeding has received much attention. Gage (1928) gave some details of the process, including observations on the clearing of the branchial basket when clogged. This was done by a sharp reversed expiration. Newth (1930) gave a very thorough account of the feeding process, to which little has been subsequently added, although it has been confirmed by duplicate observations (Schroll, 1959). Mucus secreted in the pharynx by the ventral endostyle is passed forward and upward in several lateral ciliated bands; these mucus strands are then dislodged at the front of the grooves by the velum and are swept backwards in the respiratory flow; these strands unite in the centre of the pharynx to form a conical net through which the incoming water must pass. The united mucus strands then pass back into the gullet, where cilia pass it on into the intestine. Schroll (1959) showed

that these mucus strands will selectively pick up diatoms and to a lesser extent detritus. Newth (1930) noted that some mucus not used in feeding issued through the gill openings, and he considered that this was used as a cement for the burrow walls. In ammocoetes removed from the sand this unused secretion may block the gills, causing death by asphyxiation.

f) Ammocoetes as Members of the Stream Community

Little has been written of relationships between larval lampreys and other stream life. Studies on feeding, notably those of Creaser and Hann (1929) and Schroll (1959), do show their place in the food chain in that they consume mainly primary producers such as diatoms and other algae. The importance of ammocoetes as food of other vertebrates has not yet been investigated in any detail. Ammocoetes are evidently eaten by many fish if they can get them, since they have been and still are extensively used as bait. Gage (1893 and 1928) describes extensive shipments for use as live bait made from Cayuga Lake; Schultz (1930) describes their use for bass and trout bait in the State of Washington, U.S.A. Vladykov (1949) describes their use in the Province of Quebec as bait for pickerel (Stizostedion vitreum), black bass (Micropterus dolomieu), muskellunge (Esox masquinongy), striped bass (Morone saxatilis), etc. Vladykov also states that they are eaten by "many valuable food fishes such as speckled trout, black bass, doré, etc." in their natural habitat. Eels (Anguilla rostrata) are also regarded as predators on larval lampreys (Perlmutter, 1951). Perlmutter (1951) did demonstrate that American eels would seek out and eat ammocoetes in aquaria; however, accounts of the natural food of the American and European eel (Anguilla anguilla) do not show ammocoetes as an item in their diet (Frost, 1946; Godfrey, 1957). Churchill (1947) considered that the larvae of L. fossor played only a very minor role in the life of the stream community. Of 300 "trout" stomachs examined in his survey, 5 contained the remains of lampreys; it was not clear, however, whether the partly digested remains were ammocoetes or of adults. None of 200 "sucker" stomachs examined contained larval lampreys.

It is evident from the literature, however, that lamprey larvae may be present in very large numbers and thus, if only on a basis of the total contribution made to the biomass of the stream, must be considered as an important constituent of the community. Churchill (1947) found L. fossor more numerous than any species of fish in the Brule River, Wisconsin, U.S.A. Other authors have given figures for maximum abundance of ammocoetes found by them; these are shown in Table III.

g) Growth and Length of Larval Life

Considerable effort by many authors has been devoted to the problem of aging larval lampreys. Since there is no bone, scale, otolith or bone reading cannot be carried out, and no other tissue has been found which lays down visible growth rings. Thus the only practical method for estimating age has been the use of length-frequency diagrams, wherein cyclic concentrations of length in a population are taken to indicate year-classes. However, this method has proved far from ideal, since such large variations in

ammocoete growth occur that sharp frequency peaks among larvae older than one year are the exception. Such variations occur not only from habitat to habitat, but within a single habitat. Some authors were unable to estimate the length of the larval period in ammocoete populations they studied, because of this variation (Dendy and Scott, 1953; Churchill, 1947). Other authors have attempted to base estimates on relatively small collections and their results must be accepted only with caution (Macdonald, 1959; Müller, 1856). It has been accepted that the most reliable method for estimation of the length of the larval period is repeated large collections from one population (Chappuis, 1939; Knowles, 1941; Hardisty, 1961, 1944; Schultz, 1930). Estimates for several species of lampreys, given by various authors, are shown in Table IV.

Repeated examination of length-frequency composition of ammocoete populations over a period of time also gives information on the rate of growth of the larvae. Hubbs (1924) drew a growth curve for E. (L.) lamottei, Okkelberg (1922) did similarly for L. fossor, and Hardisty (1961) has recently published similar data for British L. planeri and Great Lakes P. marinus. Hardisty (1961) was able to show that growth up to the start of metamorphosis was almost linear in general nature, a fact which adds confidence to limited extrapolation of existing data. Hubbs (1924), however, showed that growth in E. (L.) lamottei he studied was sigmoid in nature, and Okkelberg (1922) showed that growth in L. fossor was also sigmoid in nature. Hardisty (1961) suggests that the length of the larval period of each species is constant, and that variations in the rate of growth result in variations in size at metamorphosis. Churchill (1947) showed that in L. fossor growth rates of male and female ammocoetes may differ, since the mean length of those two groups differed during metamorphosis. This factor may complicate the growth picture in other species.

h) Methods of Collection of Ammocoetes

Many methods have been used to collect ammocoetes, but perhaps the most widespread method has been by digging mud from the river bed and then depositing it on the bank where the ammocoetes wriggle to the surface (Gage, 1893; Maskell, 1929; Chappuis, 1939; Schroll, 1959). A slight modification of this method, wherein the bottom was dug up using a dip net which exerted some sifting action, was employed by Schultz (1930) and Knowles (1941). Léger (1920), exploiting the free-swimming activities of ammocoetes, used small hoop nets. Enequist (1937), working in Swedish rivers, employed a very novel method; he used rotted potato peelings spread on the river bed to bring out the larvae. In recent years, however, the use of the electric shocker for ammocoete collection in shallow water has become almost universal. Churchill (1947) used this method as early as 1945, and Applegate (1950) used it in his extensive survey of the Ocqueoc River.

The use of electricity in fish collection is now such an important tool that its development deserves special mention.

Denzer (1955), who carried out a thorough study of electro-fishing, pointed out that the study of the reactions of organisms to electricity began

in 1843 when Unger (1843) carried out experiments with protozoa and algal spores. Many subsequent workers have added to this initial work; notable among these are Fr. and Fe. Scheminsky (various papers, 1922-1941) and Holzer (1932). However, the real "father" of practical electro-fishing is Schoenfelder (1925), whose findings were published under the title of "Fishing with Electricity." In North America electricity has been extensively used in stream survey work, and has also been used as a barrier to prevent fish migrations. Applegate, Macy and Harris (1954) published a selected bibliography on the applications of electricity in fishery science which lists most of the important work up to the end of 1953. Since that date, Rollefson (1958) has published an important account concerning direct current electro-fishing. The use of electrical devices to control sea lampreys in the Great Lakes has been described by several authors (Applegate, Smith and Nielsen, 1952; Kennedy, 1957). Much work of practical importance in the use of electricity in shocking lampreys has been carried out by McCauley (1960). McCauley showed that in water of low conductivity, such as that flowing off the Canadian Shield, a greater voltage gradient must be applied to the water than in the more conductive water typical of southern Ontario.

Recently ammocoetes have been sought in deeper water than that in which normal electro-fishing techniques can be used. For this purpose, Stauffer and Hansen (1958) used Peterson and orange-peel dredges, and Thomas (1960) used a specially-designed anchor dredge.

i) Identification of Ammocoetes

In a study of this nature it is essential that all ammocoetes encountered can be assigned to their correct genus and, if possible, species. Literature dealing with the identification of Ontario ammocoetes is therefore reviewed in some detail.

Lampreys of four species have been found in Ontario. These are: Ichthyomyzon unicuspis, the silver lamprey; Ichthyomyzon fossor, the Michigan brook lamprey; Petromyzon marinus, the sea lamprey; and Entosphenus (Lampetra) lamottei, the American brook lamprey. Throughout much of Ontario all four species occur together. E. (L.) lamottei is, however, absent over part of the north shore of Lake Superior. Various keys (Vladykov, 1949; Hubbs and Lagler, 1958; etc.) are available for separating adults of these species on a basis of dentition and fin arrangement. Separation of ammocoetes, however, presents more of a problem and, in fact, no key exists to separate ammocoetes of the two species of Ichthyomyzon, although Vladykov (personal communication) is currently working on such a key. Ichthyomyzon ammocoetes are normally separated from the other genera on a basis of myomere counts. In North America the myomeres are normally counted between the last (7th) gill opening and the anterior tip of the cloacal slit (trunk myomeres) (Hubbs and Trautman, 1937); however, certain authors (Raney, 1941) have counted them to the posterior end of the cloacal opening, giving counts 2 to 3 myomeres higher. Various European authors (Cotronei, 1927; d'Ancona, 1930) have counted preanal myomeres from the eye to the cloaca and therefore give much higher figures.

Using the Hubbs and Trautman (1937) method, Vladykov (1949) gives the myomere count for the four species as shown in Table V.

Thus, Ichthyomyzon spp. are distinguished from Petromyzon and Entosphenus. The fewer number of trunk myomeres in Ichthyomyzon spp. is reflected in their greater relative width than in the other two species. This character is quite obvious in living ammocoetes and may be used to separate them after some experience is gained. A second character, which will also separate these two groups, is the presence of two dorsal fins separated by a sharp notch in Petromyzon and Entosphenus, whereas in Ichthyomyzon spp. there is a single dorsal fin. This second character, however, cannot be used for ammocoetes smaller than 40 millimeters (Vladykov, 1960), as all ammocoetes smaller than this have but a single dorsal fin.

Another rough guide which is useful after experience in separating the three genera is overall colour. This may be described as grey-brown in Ichthyomyzon, blue-grey in Petromyzon, and yellow-grey in Entosphenus; these differences are most apparent in larger ammocoetes.

Ammocoetes of Petromyzon marinus and Entosphenus (Lampetra) lamottei have been fully described in two papers by Vladykov (1950 and 1960), the first describing ammocoetes larger than 60 millimeters and the second the smaller ones.

The main character used in identification of the larger ammocoetes is the pigmentation pattern in the integument. In smaller individuals interior pigmentation is also useful.

Pigmentation patterns for ammocoetes over 60 millimeters are described in detail by Vladykov (1950) and may be summarized as follows:

Caudal fin: P. marinus - pigmentation from notochord to extremity of caudal rays; E. (L.) lamottei - pigmentation along notochord only.

Caudal peduncle: P. marinus - lower edge pigmented; E. (L.) lamottei - unpigmented.

Branchial region: P. marinus - upper part well pigmented; pigmented cells often descend to the horizontal groove; E. (L.) lamottei - there is a wide unpigmented band above the horizontal groove equal to about two widths of branchial myomeres.

Upper lip: In P. marinus the pigmented area extends almost to the lower edge; in E. (L.) lamottei the lower half of the lip is without pigment.

Several other morphological characters are also distinctive. The shape of the caudal fin is in P. marinus rounded and distinctly "beaver tail" like; in E. (L.) lamottei the tail is somewhat pointed and the upper outline is elevated and obtusely angled, while the lower edge is smoothly curved. There are also differences in the shape and pigmentation of the precursor

of the tongue. This however, is not a character which can be used without dissection.

The aforementioned pigmentation and tail shape characters can all be discerned with the naked eye in ammocoetes over 60 mm. A dissecting microscope is often necessary with smaller animals, particularly those less than 30 mm in length. Vladykov (1960) gives detailed descriptions of ammocoetes of P. marinus and E. (L.) lamottei from 19-68 mm in length. The principle differences are in the intensity and pattern of pigmentation. The most important area is the dorsal surface of the head and trunk; within this general area several points are of prime importance. The post nostril non-pigmented area is in P. marinus typically smaller than the nostril, whereas in E. (L.) lamottei it is about twice the size of the nostril.

The cephalic dark line is situated in the cartilaginous brain capsule and is easily seen in E. (L.) lamottei and in P. marinus up to about 30 mm in length; in larger P. marinus it is obscured by skin pigmentation.

Cephalic oblique muscular septa: These septa are quite pronounced in P. marinus due to regular pigment cells along them. In E. (L.) lamottei large and irregularly placed pigment cells almost completely mask the septa.

Mid-dorsal band: This non-pigmented band is wider in E. (L.) lamottei than in P. marinus. Typically, in P. marinus it is narrower than the space between the first two gill openings when measured at the level of the 5th gill opening. In E. (L.) lamottei it is typically wider than this distance.

The lateral side of the head is also an important area.

The upper lip in P. marinus has relatively abundant chromatophores extending quite close to the lower edge; in E. (L.) lamottei usually more than the lower half remains unpigmented.

Branchial region: In P. marinus the chromatophores extend almost down to the gill openings, whereas in E. (L.) lamottei there is a very wide unpigmented band above the openings.

As in the larger animals, pigmentation of the tail region may be useful.

Caudal peduncle: In P. marinus pigmentation extends over the entire peduncle, whereas in E. (L.) lamottei there is always an unpigmented band along the lower edge.

Caudal fin: Chromatophores are present along both dorsal and ventral edges of the notochord in P. marinus, but in E. (L.) lamottei these are absent.

One or two percent of sea lamprey ammocoetes caught, and perhaps the odd American brook lamprey, are very much lighter in colour than normal. This pale coloration is caused by complete contraction of all chromatophores (and possibly a reduction in their number). It is possible that this form may be caused by a physiological disorder rather than by a morphological difference. Young (1935) has described the normal rhythm of colour change in larvae of Lampetra planeri. The chromatophores are normally contracted during darkness. Removal of the pineal complex resulted in the melanophores remaining in the expended position. Such expansion could also be elicited by injection of pituitrin. It was, therefore, concluded that paling of ammocoetes was due to inhibition of the posterior pituitary secretion by nervous impulses set up by the changes in illumination of the pineal complex. Some malfunction of this system could presumably also be the cause of light-coloured ammocoetes encountered.

MATERIALS AND METHODS

a) Shocking Equipment and Methods

1) Shocking Equipment

The equipment used for shocking has been developed here and consists essentially of a 110v. A.C. generator connected to a pair of paddles, one of which is equipped with an interrupting switch. The details are as follows:

Power Supply: Bendix Model 110 portable A.C. generator supplied by Bendix Aviation Corp. The generator is a compact unit, measuring 19 inches long, 13 inches wide and 11½ inches high, weighing 43 pounds. It is powered by a 2-hp, 2-cycle air-cooled gasoline engine. The output is 750 watts at 110 volts, 60 cycles. This unit has proved to be very satisfactory for shocking purposes, being very reliable and small and light enough to be carried easily by hand or in a small boat or canoe. The power output is more than enough for all shocking requirements. The cost of the generator was about \$313.

Shocking Paddles: The paddles used in shocking have been developed at the London Station. They have been altered several times to produce the present version. The unit consists of two paddles, one held by the operator and the other either stuck into the bottom and left or attached to the operator's belt (stationary electrode) and dragged behind (depending on water conductivity). The two paddles are connected by 30 feet of 16/2 type S (heavy duty) cable. The plug for connection to the power source is located at the top of the stationary electrode, and one wire is connected directly to the spade-shaped metal end of the paddle. The operator's paddle is equipped with a normally open micro-switch in a water-proof rubber covering on the handle and with a metal kitchen-type food strainer 8 inches in diameter with a fine mesh on the end. This serves both as a net and as the electrode. The strainer is easily and quickly replaceable with standard inserts. Also incorporated in the handle of the operator's electrode is the neon indicator of a built-in test circuit. Figure 1 illustrates the electrode circuit. The neon indicator lamp

will only light when voltage is present across the two electrodes. It will therefore indicate a fault in the switch or wiring. This indicator is a valuable part of the equipment, since it is difficult to tell without it whether voltage is present, and one may work for a considerable time without realizing the fault.

The complete electrical system on the operator's electrode, with the exception of the sieve, is completely waterproofed, an essential safety precaution, since when working in water the apparatus is often wet and may even be immersed.

Extension Cord: Although this is the most simple part of the whole apparatus, it can, if not well organized, cause much waste of time. The extension itself is of 16/2 S type (heavy duty) cable, 300 feet in length. Various types of reel have been tried; the most successful has been a heavy-duty hose reel set on a broad-based frame of steel tubing. The power source end of the cable is provided with a plug which is fastened at the centre of the hose reel. This is connected to the generator by a separate small extension which must be disconnected whenever wire is extended or re-wound. This equipment is illustrated diagrammatically in Figure 2. "Twist lok" receptacles and plugs are used at all connections and save accidental disconnections from vibration or pulling.

Figure 3 illustrates the entire shocking equipment, and Figure 4 shows more detail of the cable reel and its operation.

Protective Clothing: Rubber boots of appropriate length for the water depth are the only protective clothing used. The boots must be kept in good order, since a minute hole which admits little water will provide a conductor and the operator will not be insulated from the water.

ii) Method of Shocking in Streams

The area to be shocked is normally marked using natural landmarks, and shocking proceeds from the downstream to the upstream edge of the area. In streams up to about 30 feet in width, the stationary electrode is driven into the substratum in the centre of the stream and 10 to 15 feet upstream of the downstream edge of the area to be shocked. The area is then "swept" by the operator. Starting at the downstream right edge of the area, the operator places the electrode at a point about 3 feet inside the area and then moves it slowly with a zig-zag motion over an area about 3 feet wide and back to the downstream limit. While the electrode is moved, the micro-switch is repeatedly and momentarily depressed and released in order to pulse the current. Figure 5 illustrates the technique. The electrode is passed over the area repeatedly in this way until ammocoetes cease to appear. The operator then moves 3 feet to his left, repeats the procedure and so on across the width of the stream. Having completed one swath in this manner, a second one immediately upstream and overlapping the first by 6 inches is cleared and so on up to the stationary electrode. The stationary electrode is then moved further upstream and the operations repeated until the entire area is covered. Figures 6 and 7 illustrate the

operation. The method is easily modified to wider streams or small areas within a stream. The rate of movement of the electrode and the rate of current pulsation are dependent largely on temperature conditions. The lower the temperature, the slower the movement and the rate of pulsation must be. Ammocoete movements are very slow at near freezing temperatures, and if care is not taken animals may be tetanized within the mud and never leave it.

When during the operation one ammocoete is observed to leave the substrate, it can usually be caught easily with the strainer electrode and may be held there against the water current while others are captured. Within the strainer the ammocoetes are not tetanized at each pulse, since the interior of the strainer forms an equipotential area (a sort of reverse Faraday cage). It is comparatively rare that an ammocoete will swim upstream out of range; however, if one is observed making off, the current may be held on for as long as it takes to cause tetanus and the ammocoete will drift down into the strainer.

The presence of a second person to make a shocking team is essential for efficient pursuance of the method and is, in addition, an invaluable adjunct in case of emergency. The second person is equipped with a second strainer on the end of a broom handle. He takes up a position from 3 feet to 10 feet or so behind the operator and catches ammocoetes that get by. The deeper the water the further behind the assistant is positioned. Most ammocoetes, when the water is above 45°F, will swim to the surface where they are most easily caught. The assistant, therefore, positions himself where the ammocoetes reach the surface. Below 45°F, many ammocoetes cannot swim strongly enough to reach the surface and are carried away along the bottom, where they are more difficult to spot. In muddy water only those reaching the top can be caught, and in such a case the presence of an assistant is doubly important. The assistant may also, if the need arises, move forward and work within the electric field; here his strainer will act as a Faraday cage and he can hold ammocoetes unharmed while the current is on. Such a procedure becomes necessary where large numbers of ammocoetes leave the mud together, particularly where the water current is slow.

Once captured, the ammocoetes are transferred directly to a suitable receptacle placed nearby on the shore. A large plastic baby bath has proved most suitable for this purpose. If the distance to the shore is large, ammocoetes are transferred to the assistant's strainer and he makes periodical trips to shore.

Polarizing glasses are often useful for increasing visibility beneath the water surface by reducing the glare of the sun off the surface.

In waters of high resistivity, such as streams draining the Canadian Shield, the shocking and stationary electrode must be maintained within about 8 to 10 feet of each other. The most satisfactory method devised has been to attach the stationary electrode to the operator's belt with one turn of the extension cord and let it drag along behind.

iii) Access to Shocking Station and Mapping of Stations

Many stations were accessible by road; those that were not were reached by an 11' 6" boat equipped with 3.5 hp motor or with no motor.

All stations were located on 4 inches to one mile maps at the time of shocking by the use of landmarks. A co-ordinate system was used for reading the position of each station in Big Creek.

b) Trapping Methods

A two-way trap weir was installed on Stony Creek, a tributary of Big Creek (see Fig. 15), and was operated from May 9, 1958 until January 20, 1959, except for a few minor interruptions. The weir was of a standard double-V type; it is shown in Figure 8. The downstream migrant weir (facing upstream) was of one-eighth-inch mesh double galvanized wire cloth with a trap of one-sixteenth-inch mesh fibreglass screening. The upstream migrant weir was of one-fifth-inch double galvanized wire cloth with a trap of one-eighth-inch mesh of similar material. Wings and traps both had skirts of fine mesh buried facing upstream in the stream bottom. The wing ends were set into the bank about 4 feet at each side and cemented and sand-bagged in place. The wings were 3 feet in height. The traps were normally cleared once each day; sometimes they were cleared twice, at dawn and at dusk. All fish and lampreys captured were identified and their numbers recorded. All lampreys captured were measured; adults were tagged. All the catch was then released so that it could continue in the direction in which it was travelling. Upstream migrants were released 100 yards above the weir.

The weir proved difficult to operate in time of flood, as the small mesh clogged very quickly with debris and required almost constant cleaning to prevent overtopping. In winter, ice tended to form on the mesh and also caused clogging; this condition led to the ultimate destruction of the installation by high water in winter. The completely iced-over weirs just before their collapse are shown in Figure 10.

Continuous water temperature records were kept at the weir site.

c) Physical and Chemical Measurements Taken at Ammocoete Collection Stations

During stream surveys, physical and chemical data were recorded on the form shown in Figure 9.

i) Meteorological Data

Wind force on the Beaufort Scale, wind direction and cloud cover were estimated. The air temperature at the time of shocking was taken in the shade with a mercury thermometer. Maximum-minimum readings and daily rainfall were recorded from instruments located in a clearing in a tract of river valley woodland, at the confluence of Big Creek and Stony Creek.

ii) Limnological Data

The dimensions of the stream bed shocked were recorded in meters and the total area in square meters. Average depth was recorded to the nearest inch. Water temperature was taken using a mercury thermometer to the nearest 0.5°F . The temperature of the substrate 3 inches below the surface was recorded in the same way. Water turbidity was estimated in terms of the depth to which bottom detail was visible. Water velocity was measured by timing suspended submerged particles over a convenient distance with a stop watch. Several determinations were usually made and an average figure recorded. Water resistivity was measured using a portable conductivity bridge designed by J. Hoy, of the Fisheries Research Board of Canada, Biological Station, London (Hoy 1959), to the nearest 50 ohms/cm^3 . pH of the water was determined using a Beckman Model #180 pocket pH meter. pH of the substrate was measured by using the same instrument in a port of the substrate brought to the surface. Dissolved oxygen was measured using the Alsterberg modification of the Winkler method; portable apparatus for this test was designed by the writer. Substrate compactness was measured on a comparative basis using a specially designed penetrometer. This instrument is illustrated in Figure 11. The force in grams required to push a 90-degree metal cone of 1-inch base into the bottom was measured. In practice, the operator applied increasing pressure to the handles until the cone slid smoothly into the bottom. At this time a reading was taken on one of the balances; the recorded reading was therefore only half of the actual force required. Hereafter in this report this force will be referred to as the compactness. The general nature of the substrate, including its content of sand, mud, and organic matter, was estimated and its particle size was investigated using a set of U.S. Standard Sieves of the following mesh sizes: 4, 6, 8, 18, 30, 60 and 200. The mesh dimensions of these sieves is presented in Table VI. A standard volume of the substrate was placed in the coarsest sieve and washed and shaken through the series. The volume of soil to the nearest tenth part of the total volume remaining in each sieve or passing through the finest was then estimated. Stratification of sediments in the bottom to a depth of 18 inches was investigated using a core sampler. Incident illumination at the water surface was measured in foot candles using a "Brockway Norwood Director" incident light meter. A second reading was taken in the open to estimate illumination from an unobstructed sky. An illumination factor was then calculated as: incident foot candles sample area/incident foot candles open sky. The factor is always fractional, proximity to unity indicating an open situation, while a small fraction indicates heavy shading.

iii) Special Measurements Taken in Big Creek

In addition to the regular data collected at ammocoete collecting stations, continuous temperature records were kept during some periods in Venison Creek and Stony Creek. In Venison Creek, continuous temperatures 4 inches below the surface of the mud were also taken for several months.

d) Handling and Measurement of Ammocoetes

1) Handling of Ammocoetes

After capture, ammocoetes were immediately transferred to water in a large polyethylene baby bath, floated in the water or placed on the bank close to the area of operation. Periodically the catch was transferred to a 5-Imperial-gallon plastic pail which was placed in a cool shady place in summer or in the vehicle in winter.

When the catch was complete the animals were either identified and measured on the spot, preserved in formalin or returned to the creek, or were transported back to the laboratory for identification and measurement. Up to 300 ammocoetes, depending on their size, were transported in each 5-gallon container.

ii) Measurement of Ammocoetes

Since Knowles (1942) showed that considerable shrinkage occurs in ammocoetes held in captivity, every effort was made to measure the ammocoetes as quickly as possible after capture. Many were measured at the stream immediately after capture; most, however, were measured in the laboratory as soon as possible after capture. Ammocoetes were measured while anaesthetized with Tricaine methanesulfonate (M.S. 222 Sandoz). M.S. 222 has been used with many poikilothermous aquatic animals. Sandoz (1958) summarizes its use with the groups Chondrichthyes, Osteichthyes and Amphibia, and Thorson (1959) has reported its use with the Agnatha. Thorson found a concentration of 0.25 grams per liter produced immobilization of adult sea lampreys in 2 minutes, 45 seconds, at 57°F; recovery took 5 minutes, 36 seconds. With ammocoetes, concentrations of 0.1 gram per liter to 0.5 gram per liter have given satisfactory results. Care must be taken in measuring ammocoetes to ensure that the body musculature is completely immobilized or slight contractions may occur causing variation in body length.

Ammocoetes were all measured from the extreme anterior end of the oral hood to the tip of the caudal fin (total length) and the lengths recorded to the nearest millimeter.

e) Experimental Methods

1) Holding Ammocoetes in the Laboratory

Ammocoetes for experimental purposes were normally obtained from Venison Creek at the start of each experiment. However, some were retained in the laboratory for limited periods before they were used. Ammocoetes that were to be used within 24 hours of their capture were kept overnight in holding boxes, with bottoms of 1/16-inch square mesh of fibreglass, which were floated in constant temperature tanks. The constant temperature tanks were supplied with a continuous small flow of tap water and compressed

air broken up by air stones. Level in the tanks was maintained at a constant height by means of stand pipes. Temperatures were set close to mean stream temperatures. For longer holding, ammocoetes were invariably kept where they had some sand to burrow into. Ammocoetes kept without substrate for periods longer than 24 hours showed abrasion of the oral hood, caused by their attempts to burrow; this injury prevented normal burrowing if they were later placed in a container with sand. Facilities for holding ammocoetes in sand were of two kinds. Large aquaria with fitted lids of fibreglass screen were provided with four inches of sand and then sunk in the constant temperature tanks previously referred to. In the second method tap water was run through a series of painted galvanized tubs similarly provided with sand. Before passing through the tubs the water was aerated and treated with sodium thiosulphate to remove the chlorine (see McCauley and Scott, 1960). No attempt was made to feed ammocoetes held in this way.

11) Apparatus for the Study of Circadian Activity Rhythms and Burrowing Activity in Ammocoetes

The apparatus for studying activity in ammocoetes consisted essentially of a small artificial stream of controlled temperature and flow set in a cabinet where illumination was similar to that outside and was set to a normal daily rhythm. De-chlorinated tap water was supplied to the stream from a constant level tank; flow was controlled by means of a variable constriction in the supply pipe to the stream. Before entering the stream, the water passed through a chamber in which heating could be carried out either continuously or with a circadian rhythm linked to that of the illumination. The stream itself was a polyethylene baby bath 24½ inches long, 15 inches wide, and 7 inches deep. About 3 inches of sand and 3 inches of water were maintained in the stream. Water level was retained at a constant level by means of an overflow. Figure 12 showed the layout of the cabinet. The positions of burrows within the stream were mapped with the aid of a grid of 1-inch squares which was laid on top of the bath. An automatic free-swimming activity recorder was used. This recorder, which was designed by J. Hoy of the Fisheries Research Board of Canada, Biological Station, London, consisted essentially of a series of 3 sensors projecting vertically into the water of the stream, which, when touched, broke an electrical circuit. These breaks in the circuit were recorded on a strip chart recorder. Figure 13 shows the activity detector in position in the stream. Water currents passing in and out of ammocoete burrows were observed, using a weak solution of fluoresceine to which the ammocoetes did not react and which could be detected even in extreme dilution with the aid of an ultra-violet lamp. Possible activity at burrow mouths during the dark hours was investigated, using a single lens reflex camera with 135-millimeter telephoto lens, extension bellows and polarizing filter. An electronic flash was coupled to the camera. A cable release enabled photos to be taken without opening the cabinet.

iii) Apparatus for Studying Burrows and "In-Burrow" Behaviour in Ammocoetes

Two specially made observation tanks were used for this purpose in a controlled illumination cabinet similar to that described above. The tanks consisted of two glass plates $17\frac{1}{2}$ inches long by $9\frac{1}{2}$ inches high, set $1\frac{3}{8}$ inches apart in a wooden frame. Six inches of sand was maintained in the tanks. It was hoped that in such confined quarters ammocoetes would on occasion construct burrows against the glass. Water flow over the surface of the sand was adjustable within wide limits so that natural conditions could be duplicated. Two such tanks were used in series.

iv) Apparatus for the Study of Swimming Speed in Ammocoetes

This apparatus consisted of a trough of galvanized iron sheet, 10 feet long, 3 inches wide, and 3 inches deep, with 2 inches of insulation on sides and bottom. A scale marked off in inches and feet ran along the length of the trough. Trials were run using water at several temperatures by timing swimming speed with a stopwatch. Both spontaneous swimming speed, which started with no artificial stimulus, and maximum swimming speed, initiated by a nip with forceps, were investigated.

AMMOCOETE STUDIES IN BIG CREEK

a) Description of the Research Area

The research area may be defined as the watershed of Big Creek, which empties into the Inner Bay of Long Point Bay, Lake Erie. Figure 14 shows the location of Big Creek in southern Ontario.

The Big Creek watershed is shown in more detail in Figure 15.

The Big Creek watershed lies mainly in Norfolk County, but some is in Oxford and Brant Counties. The total area of the watershed is about 179,800 acres of which roughly 85% is cleared, 15 % is woodland and 1% is scrub. The watershed lies almost entirely within the Deciduous Forest Region and enjoys a moderate climate. Woodland is mainly of silver-maple, white-elm type, but there are also quantities of the white oak, black oak, red oak and beech, sugar maple associations (Anon., 1953). Agricultural land in the watershed is largely of the sand plain type and is mainly used for tobacco production.

Big Creek rises in the moraine a few miles south of Woodstock, in a total length of 55 miles it falls over 375 feet to Lake Erie. At first its course is easterly and in the first 10 miles it drops 150 feet without, however, forming any significant valley. The stream then turns southward and wanders several miles over the wide plains of deltaic alluvium in Burford Township before, at Teeterville (see Fig. 15), its gradient increases and a valley begins to form. Figures 16 and 17 show typical stretches of Big Creek as it flows through the Burford Township plains. Figure 16 shows the river where

it first enters the plains, and Figure 19 is typical of the central portion of this area. At Teeterville a dam (Fig. 18) has created a shallow lake (Fig. 19). The dam, some 12 feet in height, forms an effective barrier to upstream migration of fish and lampreys. From Teeterville to Delhi, about 9 miles downstream, the river has a fair gradient and bottoms are typically of sand with some stony rapids. The velocity of flow, however, is rarely over 2 feet per second. Figure 20 shows a typical stretch of river in this portion. At Delhi the river valley is about 75 feet deep, a depth which it maintains until within a few miles of its outlet into Inner Bay. At Delhi another dam, which is shown in Figure 21, has been erected across the river. This dam, with a vertical fall of about 5 feet, also constitutes a barrier to the upstream migration of fish and lampreys. Between Delhi and Walsingham (see Fig. 15), a distance of about 19 miles, most of the remaining drop in Big Creek takes place, the gradient averages 6.5 feet per mile. Bottoms in this stretch are typically sand with some silted pools and eddies; however, for about 2½ miles below Delhi the river runs through intermittent strata of gravel and there are many short rapids with interspersed silted stretches. These rapids form spawning sites for all species of lampreys. Figure 22 shows a riffle used as a spawning site by lampreys. The rapids in this section have water velocities up to 2 feet per second, but the pools between probably have velocities below 8 inches per second. Below this gravelly reach, bottoms are typically of sand, as shown in Figure 23, and velocities average about 8 inches to 11 inches per second. Below Walsingham the gradient of the river is very slight, the course is meandering and the bottom of mud, as shown in Figure 24. Water velocity is frequently below 5 inches per second. Much of the watershed of Big Creek is cultivated and consequently during periods of heavy rain the level rises rapidly and the water becomes loaded with suspended sediment. Overtopping of the banks, particularly at spring run-off time, is not uncommon.

Several tributaries of importance enter Big Creek. About half a mile below Delhi, North Creek enters Big Creek from the west. Flow in North Creek is almost equally divided between the north and south branches. However, the two branches are of very different nature. The north branch, flowing southeast (see Fig. 15), has one of the steepest gradients of any sizeable stream in the watershed, averaging 20 feet per mile, and much of its course flows over gravel rapids with average velocities of up to 2 feet per second. The south branch, on the other hand, has an average gradient of 12.5 feet per mile and has sand bottoms over much of its length. There are, however, some rapids in its course. A dam in the north branch, shown in Figure 25, does not act as a barrier to larger lampreys and fish, but may do so to smaller species.

Another important tributary, Stony Creek, enters Big Creek from the east about 3½ miles downstream from Delhi. In this stream the average gradient is about 16 feet per mile. Much of the upper reaches flow through farmland and have sandy or muddy bottoms. Towards Big Creek, however, the gradient steadily increases and gravel bottoms are the general rule. Figure 26 shows a typical rapid. Lampreys, particularly *P. marinus*, spawn in large numbers in this stream. This is the only large tributary in which flow is really torrential at any point, water velocities exceed 3 feet per second in some stretches.

Cranberry Creek, entering Big Creek from the west some 6½ miles below Delhi, has bottoms mainly of sand and average velocity of the order of 8 inches to 11 inches per second. A steep chute, shown in Figure 27, close to its mouth has a drop of about 15 feet and provides an effective barrier to upstream migration.

Venison Creek (see Fig. 15) is the largest tributary of Big Creek. It joins Big Creek from the northwest about 7.5 miles above Inner Bay. Venison Creek is very different in nature from Big Creek in that the gradient is in general much steeper. Venison Creek runs about 14 miles from its source to Big Creek; it is interrupted by a dam about 10 miles from its mouth. This dam is shown in Figure 28. Above the dam the gradient is 8.5 feet per mile and water velocities are mainly in the range of 8 inches to 1 foot per second, bottoms are mainly of sand. Below the dam for about 4.6 miles the stream is quite rapid, the gradient averaging 19.5 feet per mile. However, although currents exceed 2 feet per second in places, gravel is rare and present only in small patches. Many of these gravel patches occur at bridges and are the result of road gravel being washed into the stream and gravel and stones tipped in to minimize erosion. These gravel patches constitute the spawning grounds for all species of lampreys. Rapid reaches in general have clay bottoms and are interspersed with sandy stretches. Silted parts, such as that shown in Figure 29, are comparatively rare and are confined to eddies, backwaters, etc. Below this rapid stretch the gradient to the mouth is less and averages 9.1 feet per mile, bottoms are generally sandy but silted pools and backwaters are extensive. Figure 30 shows a typical reach in this stretch. Unlike Big Creek, much of the course of Venison Creek is wooded. The Creek's reaction to rain is not as violent as that of Big Creek and flooding is rare.

Table VII summarizes the main characteristics of Big Creek and its major tributaries.

b) Physical and Chemical Characteristics of Study Streams

i) Chemical Data

Big Creek flows almost in its entirety through the Norfolk Sand Plain in the Huron and Erie Lowlands. Sediments of this region contain considerable amounts of calcium and consequently waters flowing over it are rather hard. In addition, water from springs which has flowed through the limestone bedrock is even harder than the surface water. Springs are common in the watershed. In several locations water is added from springs containing much H₂S, but this water is relatively small in total volume and its effect is soon lost.

Oxygen determinations were carried out at many ammocoete sample stations; however, since concentrations were in all cases close to saturation point or even above in fast reaches, it would not appear to be a limiting factor.

pH was also measured on many occasions at ammocoete collection

stations and was shown to be fairly stable. The mean pH in Big Creek was 7.99, with a range of 7.8 to 8.2; in Venison Creek the mean was 8.12, with a range of 7.8 to 8.4. pH was also measured in the surface of the substrate and there the environment proved to be somewhat less basic, averaging 7.43 with a range of 7.2 to 7.7 in Big Creek, and 7.0 with a range of 7.4 to 8.4 in Venison Creek.

ii) Physical Data - Resistivity

Many resistivity readings have been taken in Big Creek and two of its tributaries, Venison Creek and Stony Creek. Big Creek itself was the least resistive water, with an average resistivity calculated from 44 determinations spaced over the year of $2370 \Omega/\text{cm}^3$ at 20°C the range of readings corrected to 20°C was $1660 - 3550 \Omega/\text{cm}^3$. During January 21, 22 and 23, 1959, there was a heavy rainstorm following a period of very cold weather. Rain water ran off the frozen land and over the surface of existing river ice. During this flood resistivities as high as $13,440 \Omega/\text{cm}^3$ at 20°C were recorded. These readings, which do not reflect actual river conditions, were not used in calculating the mean resistivity of Big Creek. In other tributaries to be discussed below, this flood showed similar effects.

In Venison Creek and Stony Creek, many more resistivity readings were taken than in Big Creek. These readings were sufficient in number to compute monthly means for these streams and thus show any seasonal trends. Figure 31 shows mean monthly resistivity readings for Stony Creek. Table VIII and Table IX give mean monthly and range data for Stony Creek and Venison Creek respectively. As shown in Figure 31, minimum readings were recorded in November and December and maximum readings in March. No explanation is offered for this annual variation, but it can be pointed out that the variation does not appear to be closely correlated with either rainfall or stream flow, both of which will be discussed below.

iii) Temperature

Temperature readings have been taken all over the Big Creek watershed when ammocoete collections have been made. These instantaneous readings, however, give only relatively little information about the normal temperature regime of the streams. To get more complete information, recording thermometers were installed in both Venison Creek and Stony Creek from July to December 1958. This period covered some of the hottest and some of the coldest weather likely to be encountered and included periods of high and low rainfall. Concurrent weather data has been obtained from the Canada Department of Agriculture, Tobacco Sub-station, Delhi, which lies fairly centrally in the watershed. Weather data from Delhi, summarized by months for the study period 1957 to 1961, are presented in Tables X-XIV. Temperature differences between the Delhi weather station and at the creeks investigated are likely to be relatively slight. Daily maxima, minima and mean temperatures were taken from the thermorecorder charts from both streams. Mean daily temperature was taken as being midway between the maximum and minimum; while this is not strictly accurate, it does mean that these temperatures may be compared directly with air mean temperatures which are calculated in a similar manner. A monthly summary of the

water temperature data from Venison Creek and Stony Creek and air temperature data from Delhi are presented in Table XV. Using this data, it has been possible to show a precise relationship between mean air temperature at Delhi and mean water temperature in the two streams. This relationship is illustrated in Figure 32. The regression lines are both significant at much less than the 1% level. The conversion equations which apply only when the resultant stream temperature is above 32°F were as follows:

Mean water temp.

in Stony Creek $^{\circ}\text{F} = 8.16 + 0.79 (\text{Mean air temp. at Delhi } ^{\circ}\text{F})$

Mean water temp.

in Venison Creek $^{\circ}\text{F} = 25.51 + 0.48 (\text{Mean air temp. at Delhi } ^{\circ}\text{F})$

It may also be shown that a similar relationship exists between daily mean temperatures with only a slight time lag. As an example of the relationship, Figure 33 depicts daily mean air temperatures at Delhi and daily mean water temperatures in Stony Creek and Venison Creek during October 1958.

It is evident that Stony Creek temperatures are much closer to air temperatures than those in Venison Creek. This is attributed to the nature of the two streams. Stony Creek water is mainly derived from surface runoff which is close to air temperature, and in addition much of its course flows through open farm land where it is little shielded from atmospheric temperature changes. Venison Creek, on the other hand, contains considerable quantities of spring water which, flowing at near constant temperatures the year round, exerts a damping effect on stream temperatures. In addition, the creek flows through a densely wooded valley which to some extent shields it from atmospheric temperature changes. In consequence of its rather buffered temperature regime, Venison Creek rarely freezes over in winter. Indeed, as reference to Figure 32 will show, ice will not form until mean air temperature falls to about 14°F. On the other hand, during hot weather Venison Creek remains comparatively cool.

Use of Figure 32 in conjunction with the weather data given in Tables X-XIV has enabled the calculation of mean monthly stream temperatures for the period 1957 to 1961. These five-year averages are shown in Table XVI and provide a good estimate of the temperature character of the two streams. It is notable that the five-year annual mean water temperature in Venison Creek is 47.8°F, whereas in Stony Creek it is 46.2°F. This difference may be significant in terms of long-term primary productivity.

From limited temperature readings on Big Creek itself, there is evidence that for 12 miles or so below Delhi temperatures are similar to those in Stony Creek. Further downstream Big Creek follows air temperature even more closely. North Creek, Trout Creek and Cranberry Creek have similar temperature characteristics to Venison Creek.

Since ammocoetes spend most of their lives buried several inches deep in the substratum, it is important to know how this habitat differs from

that of the stream. It should be pointed out, however, that since ammocoetes draw a stream of water into their burrows, they form a micro-environment of their own which probably differs temperaturewise from both stream and substratum. To gain some knowledge of the possible temperature difference 4 inches down in the bottom, thermorecorder records were made in Venison Creek both above the bottom and 4 inches into it. It was shown that the temperature in the substratum followed stream temperature, but did not fluctuate so widely as shown in Figure 34, which shows two thermorecorder records for the period August 7 to August 14, 1958 from Venison Creek. The upper record was made in the water and the lower one 4 inches in the muddy sand. This difference may serve to insulate ammocoetes from violent temperature changes. In very cold weather when water temperature was virtually constant, there was no significant temperature difference 4 inches down in the mud.

iv) Flow in the Big Creek Watershed

Instantaneous flow estimates have been made on many occasions during the surveys of the Big Creek system. However, these estimates give relatively little information concerning mean flow and variations in flow. Daily records kept over a long period provide the only method of obtaining reliable information. Such records have been taken for several years at two points on Big Creek, Delhi and Walsingham, and in the North Branch of North Creek at Delhi by the Water Resources Branch, Department of Northern Affairs and Natural Resources. In addition, intermittent records over several years have been made near the mouth of Venison Creek. A summary of the readings for Big Creek and North Creek averaged for months for the period 1957 to 1961 are presented in Table XVII. For Venison Creek the mean flow from scattered determinations is 46.81 second feet; however, this is very likely about 25% over the time average, since average flow for Big Creek calculated just from measurements taken on the same day as the Venison Creek measurements overestimates its flow by about 25%. As noted by Russell (1962), flow in Venison Creek averages about 21% of that in Big Creek at Walsingham.

Flow measurements of other streams are not available; estimates based on known flows in other streams have however been made. Table XVIII gives data for mean flow, mean maximum flow and mean minimum flow derived from data and from estimates.

Flow reaction to high rainfall is most violent in the smaller streams, e.g., in the north branch of North Creek the ratio of mean maximum flow to mean minimum flow was 102:1; in Big Creek at Delhi it was 81:1; and at Walsingham 17:1. It is considered that the daily flow measurements for North Creek provide a reliable index of stream flow in other tributaries.

In all watershed streams, except those fed solely from springs, there is a regular annual flow cycle. Figure 35 shows the yearly flow cycle in Big Creek and North Creek (north branch) at Delhi drawn from data averaged from 1957 to 1961. The differences between this cycle and that for stream resistivity as shown in Figure 31 are considerable. Maximum flow occurs

in March and April and minimum flow in July, August and September; a second small increase in flow has been observed in December. Flow does not appear to be closely correlated with rainfall.

c) Growth and Length of Larval Life

Although much time has been devoted to growth and length of larval life of ammocoetes in the Big Creek system, this subject will only be considered here in sufficient detail so that correlations of age with size given below may be understood.

Estimates of the duration of the larval period have been made using length-frequency diagrams of large samples repeated many times. As discussed in the literature review, this method is the most reliable one available, but even so is far from satisfactory.

The samples obtained have only been in sufficient quantity for two of the four species present in the watershed and even for these species, P. marinus and E. (L.) lamottei, large samples have only been obtained from Venison Creek. A further complication arises from the fact that very few newly-transformed P. marinus or even large ammocoetes have been caught in Venison Creek. The only reliable data on the size of newly-transformed P. marinus has been obtained in Stony Creek.

The mean size of 64 newly-transformed P. marinus taken in the fall of 1958 at the Stony Creek weir was 152.7 millimeters, with confidence limits on the mean at the 95% level of 150.0 millimeters to 155.4 millimeters. The frequency distribution of this sample appears unimodal.

The mean size of 52 newly-transformed E. (L.) lamottei taken in Venison Creek from 1957 to 1961 was 173.46 millimeters (95% confidence limits 169.6 to 177.3 millimeters).

Thus it is evident that E. (L.) lamottei reach a larger size before metamorphosis than P. marinus. Since some shrinkage in size takes place at metamorphosis, it is probable that ammocoetes reach an average size some millimeters larger than the newly-transformed specimens, although such large ammocoetes are rare.

Figures 36 and 37 show specimen length-frequency diagrams for P. marinus and E. (L.) lamottei caught in Venison Creek. These particular samples show age classes more clearly than most. Many such diagrams were drawn, mainly from 15 collections of a total of 2051 P. marinus and 2953 E. (L.) lamottei taken from February 10, 1960 to October 19, 1961 at Concession #12 (N. Walsingham Twp.) road at Venison Creek, and 56 collections of a total of 3596 P. marinus and 2633 E. (L.) lamottei taken from July 3, 1957 to December 15, 1960 at Concession #9 (N. Walsingham Twp.) road, Venison Creek. In addition to these large collections, other limited collections were made higher upstream in Concession #13 and lower downstream at Concession Road #8 and Concession Road #5. Using persistent length-frequency peaks from diagrams drawn from these collections, growth

curves for ammocoetes for the first two and one half years of their lives can be drawn in detail and growth in later years estimated. Figure 38 shows growth curves for three year-classes of P. marinus drawn mainly from collections made during 1960 and 1961 at Concession #12 road, Venison Creek. Using the same diagrams, a growth graph for the life span of the ammocoetes may be drawn by plotting the positions of all reliable peaks. Such a graph for P. marinus in Venison Creek is shown in Figure 39. It is notable that while mean growth is almost constant for each year of larval life, as shown in Figure 39, growth rate during the course of the year is quite variable; maximum growth occurring in June-July and September-October; little, if any, growth occurs in early winter or early spring and actual shrinkage was observed in mid-winter. Extrapolating in Figure 39, transformation would be expected in the fifth year of life for average ammocoetes.

Soon after hatching, E. (L.) lamottei are readily distinguishable from ammocoetes of P. marinus on a basis of size alone, as shown in Figure 40, a length-frequency diagram of a catch of young-of-the-year ammocoetes made in Venison Creek on August 24, 1961. At that time, E. (L.) lamottei ammocoetes averaged 26 millimeters, and P. marinus 14 millimeters. This difference in size of the two species at similar age continues throughout the ammocoete period. Figure 41, drawn in exactly the same way as Figure 38, shows this difference. Like P. marinus, E. (L.) lamottei shows rapid growth in summer and some shrinkage during winter. Figure 42 for E. (L.) lamottei is comparable to Figure 39 for P. marinus. It is evident that although E. (L.) lamottei is larger than P. marinus when newly transformed, transformation length is reached one year earlier. It appears most probable that E. (L.) lamottei has a larval period of 4½ years on the average.

It must be emphasized that all the foregoing data is based on average ammocoetes. References to Figures 36 and 37 show that the size range within each year class is considerable and increases with age in both species. By the end of the first year of life, the largest individuals of age class one are as large as the smallest individuals of age class two. This overlap rapidly increases with age. The extent of this overlap makes it appear probable that some individuals of both species may reach transformation size two years before the average specimens transform, and P. marinus may reach 9½ years old before transformation, while some E. (L.) lamottei may reach 7½ years. This is illustrated diagrammatically in Figures 43 and 44.

d) Macro-distribution of Ammocoetes

Most of the data collected concerns P. marinus and E. (L.) lamottei; however, some Ichthyomyzon spp. were collected and information concerning their distribution is included.

One of the basic factors determining the broad distribution of ammocoetes in streams is the location of spawning sites. For P. marinus spawning sites in Big Creek have been investigated in detail; these sites are shown in Figure 45. E. (L.) lamottei also spawn in the same areas as sea lampreys, but also have additional spawning sites. Adult sea lampreys are halted in Big Creek at Delhi Dam (Fig. 21), Venison Creek Dam (Fig. 28)

and Cranberry Creek chute (Fig. 27). These barriers are also marked on Figure 45. In the case of the American brook lampreys, adults do not migrate to the lake and consequently populations are maintained above barriers. Some downstream migration of E. (L.) lamottei does, however, occur as will be discussed below, resulting in loss of individuals to populations above barriers. It appears quite possible that smaller obstructions would be a barrier to E. (L.) lamottei adults rather than sea lamprey adults, because of their smaller adult size. The North Creek Dam (Fig. 25) may be a barrier to migrating adult E. (L.) lamottei; some evidence for this is given by the fact that large numbers of this species may be collected under the dam during the spawning season. Teeterville Dam (Fig. 18) on the main river would certainly constitute a barrier to migration of E. (L.) lamottei and Ichthyomyzon spp. adults.

The distribution of P. marinus, E. (L.) lamottei and Ichthyomyzon spp. ammocoetes as determined in the shocking survey is shown in Figure 46. Sea lampreys were generally distributed below the spawning sites (Fig. 45). They did not occur in any tributaries where spawning did not take place, except right at the mouths. In Big Creek itself, P. marinus ammocoetes were present immediately below the dam at Delhi and were caught at many stations downstream to Walsingham. It must be assumed that they also occur below that station, however; for reasons to be discussed below, adequate sampling in the very slow reaches below Walsingham is a problem. In North Creek (north branch) sea lamprey ammocoetes were found high upstream where the stream was very small. In Stony Creek, too, this was the case, ammocoetes being found upstream to a point where the creek had a mean flow of less than 1 cubic foot per second and averaged only 2 feet or so in width. In Venison Creek, P. marinus was not found higher upstream than about 2 miles below the dam. Nevertheless, they are almost certainly present as high upstream as the dam, as spawning has been observed immediately below this structure. Below 2 miles below the dam, P. marinus was ubiquitous in Venison Creek. As shown in Figure 46, both E. (L.) lamottei and Ichthyomyzon spp. were much more widely distributed. E. (L.) lamottei was present in several small tributaries with mean flows below 1 cubic foot per second, but curiously was absent from other tributaries which appeared suitable. Such tributaries are marked X in Figure 46. Even more peculiar was the scarcity of E. (L.) lamottei in Stony Creek which has large populations of sea lampreys. However, E. (L.) lamottei was the most widely distributed species of lamprey in the watershed.

In regard to individuals identified as Ichthyomyzon, it is suspected that the distribution of I. unicuspis is similar to that of sea lamprey, and that the Ichthyomyzon spp. found elsewhere were I. fossor. I. unicuspis spawns in similar locations to P. marinus.

e) Detailed Distribution of Ammocoetes

1) Factors Controlling Detailed Distribution

In order to investigate the factors controlling variations in population density of ammocoetes in Venison Creek, a survey was conducted by shocking

stations at one quarter mile intervals in the stream; 47 stations were examined. Each station consisted of as much stream bed at each location as could be reasonably considered a uniform environment in respect to the factors under study. Stations examined ranged in area from 45 square meters to 2 square meters and averaged 10.3 square meters. At each station, water and bottom temperature, water velocity, depth, illumination factor (incident light in foot candles at water surface/incident light in foot candles on open ground), resistivity, water and bottom pH, O₂ % saturation, bottom compactness and bottom particle size, and its general nature were measured and recorded. The results are presented in Table XIX in the Appendix. The resulting figures were compared with population density of P. marinus and E. (L.) lamottei.

The most obvious feature of the data is the similarity between population densities of P. marinus and E. (L.) lamottei. P. marinus was somewhat more abundant on the whole with an average population density of 1.75 per square meter; E. (L.) lamottei averaged 1.43 per square meter. Fluctuations in population density at different stations was closely paralleled in the two species. The correlation coefficient "r" for their population densities was +0.77 (46 degrees of freedom).

For several of the factors measured, it was at once clear that there was little, if any, correlation with ammocoete abundance. Several factors were almost constant during the survey, e.g., resistivity, water and bottom pH, and O₂ saturation, and obviously were not important. Temperature, although it showed considerable variation, was also clearly not a controlling factor in this stream, as each station must have experienced a similar temperature regime.

Several other factors, although they proved to have little effect on population density, warrant fuller results being presented in view of the importance attached to these factors by other authors.

Schroll (1959) and Bams (1958) both state that ammocoetes live in shaded locations. However, in Venison Creek the correlation between population density and illumination factor was negligible ($r = +0.028$, 46 degrees of freedom, for P. marinus).

Many authors have stated that ammocoetes were more abundant in shallow water. In Venison Creek there was very little evidence for this view, the correlation coefficient "r" for P. marinus population density and depth being -0.177 (46 degrees of freedom).

Almost all authors discussing ammocoete distribution mention the prevalence of them in muddy patches with slow water velocity. In Venison Creek these two factors appeared to be the main ones controlling distribution and have been investigated in detail. Since the two factors are to some extent inter-related, they will be treated together. Table XX lists correlation coefficients for all combinations of species and factors. Thus the inverse relationships between population densities and both velocity and compactness are clear in both species. It was curious, however, that there was no clear

invariable relationship between velocity and compactness. Such a relationship was often clear at individual stations, but the presence of soft bottom with low water velocity was not universal. As this was the case, a multiple regression of population density on compactness and velocity was tested. For P. marinus the multiple correlation coefficient "R" was 0.47 and for E. (L.) lamottei 0.45 (45 degrees of freedom); in both cases somewhat better values were obtained than with either of the corresponding simple correlation coefficients (see Table XX).

P. marinus

$$Y = 5.56 - 0.025 X_1 - 2.723 X_2$$

E. (L.) lamottei

$$Y = 3.53 - 0.010 X_1 - 1.77 X_2$$

where Y = population density, individuals per m².

X₁ = compactness in g/10.

X₂ = water velocity in feet per second.

Thus, ammocoetes of both species were found to be most abundant where water velocity was very slow and the bottom very soft.

The general nature of the bottom and its particle size is also related to ammocoete abundance; however, these two factors are described in the terms of the two parameters used. Mud where ammocoetes are abundant is usually soft and deposited in areas of low water velocity; it has a small average particle size. Coarse sand, on the other hand, wherein ammocoetes were quite rare only occurs "as a rule" where water velocities approach 1 foot per second, and such deposits have larger particle size and are firmer. Anomalies arise when changes in flow pattern leave deposits typical of higher water velocities in regions of low velocity. The presence of organic matter, which has often been associated with ammocoete abundance in the literature, was also found to be associated with low water velocity.

ii) Ammocoete Beds

Ammocoetes in certain streams are most abundant in certain well-defined areas. The term "ammocoete beds" has been coined to describe such places. In Venison Creek it has been shown that these ammocoete beds are typically places of low water velocity and soft bottom. In the middle reaches of Venison Creek between the dam and about 3 miles from its mouth where the gradient averages about 15 feet per mile, concentration of ammocoetes in such beds is the general rule, since the mean velocity of the stream is between 8 inches and 1 foot per second and only fairly coarse sand is able to settle in the main flow. A typical part of Venison Creek with these characteristics lies in the downstream portion of Concession #13, N. Walsingham Township. This portion of the creek is shown in Figure 47,

which gives details of ammocoete bed positions and current flow directions. The beds shown in the figure may be divided into 3 typical groups. Beds "A", "B", "E", "J" and "L" were composed mainly of sand and were transitory in nature, being frequently destroyed by high water and subsequently re-formed. "C", "D", "H", "I", and "K" were of finer sediments and slower water velocity than the first groups and had more organic matter. Water velocity was typically 0.1 foot per second, compared with about 0.5 foot per second for group one. Compactness averaged <500 grams for group two and >500 grams for group one. These beds were fairly permanent in nature. Beds "F" and "G" constituted a special case and were caused by the construction of a small beaver dam which backed water up, reducing its velocity and allowing soft sediments to settle. Frequent damage to the beaver dam resulted in destruction of these beds and the one downstream of the dam was constantly changing shape with each repair of the dam. Both these beds were variable in consistency, but the softest sediments were generally to be found at the upstream side of the dam.

In the lower 3 miles of the course of Venison Creek the mean water velocity falls below 8 inches per second, and fine soft sediment settles over the entire stream bed. In this section no ammocoete beds as such occur, the larvae are fairly evenly distributed. Such a location is shown in Figure 30.

One particular ammocoete bed in the upstream part of the course of Venison Creek in Concession #8, North Walsingham Township, has been studied in detail and observed from 1957 to 1961, and was also used in migration studies. Figure 48 is a sketch map of the locality showing the position of the "bed" in relation to adjacent terrain. The "bed" was a typical one situated on the inside of a stream bend and by-passed by the main current. Depth of water over the bed ranged from 2 feet at its outer edge to zero at the bank and averaged about 9 inches. Water current at average flow varied from almost nothing near the bank to $\frac{1}{2}$ foot per second at the outer edge. At times of flood, average depth would increase up to 2 feet and current over the bed to over 1 foot per second. The bed consisted of at least 18 inches of sand with a small mixture of organic matter.

The bed proved to be quite stable during the five years of observation. During this period it was only observed to "wash out" on one occasion. This, in February of 1958, was a period of high water accompanied by floating ice. On February 6, 1958 the "bed" had completely disappeared and had been replaced by a depression 3 feet in depth at the center. It seemed probable that this "wash out" was caused by a change in the path of the main current flow caused by an ice dam and not by mere high water. Supporting evidence for this conclusion is the fact that the "bed" has remained relatively constant in position and composition despite many other floods during the observation period. Following the "wash out", the bed was rapidly rebuilt by natural sedimentation and re-colonized by ammocoetes.

From July to November 1958, a detailed study was made of the bed. Usually at weekly intervals measurements were taken of compactness, water velocity, composition of the sediment and illumination. Continuous

temperature records were kept. The results are presented in Tables XXI and XXII. Inorganic sediments normally comprised over 75% of the volume of the bed and were of fine sand. These sediments were normally held in virtually equal quantities by sieves #60 and #200 and therefore ranged in size from 0.59 millimeter diameter to 0.074 millimeter. However, on some occasions proportions in these two sieves varied. Ratios of percentage of total soil volume in sieves #60 and #200 varied from 60:30 to 10:56. The amount of organic matter in the bed was normally less than 15% (by volume), except during fall when leaves made up to 30% of the total volume. The normally present organic matter lodged mainly in the sieves #18 and #30 and therefore had a particle size of between 2.38 millimeters and 0.59 millimeter. Leaves were mainly larger than $\frac{1}{4}$ inch and most remained in sieve #4.

The compactness of the sediments forming the bed was fairly stable. Maximum compactness was never below 1000 grams and averaged just over the maximum 2000-gram reading of the penetrometer. Minimum readings were more variable, ranging from 200 grams to 1800 grams; however, areas of very soft sediment were usually limited in area and normally situated on the outer and extreme downstream edges of the bed. It is considered that these soft sediments were transitory on the bed and were normally only deposited when flow was less than average. Mean compactness was fairly stable, ranging from 800 grams to just >2000 grams. By way of comparison, shore sediments examined (to be discussed below) ranged from 300 grams to >6000 grams. Sediments encountered in a general survey of Venison Creek ranged from 0 gram to >2000 grams, and compactness averaged about 700 grams. It would seem therefore that the ammocoete bed at Concession #8 was somewhat harder than the average sediment.

A regular variation in the pattern of ammocoete distribution within the bed took place associated with changes in flow in the stream. During average to low water states, ammocoetes were found to be fairly evenly distributed across the bed. As water flow increased and in consequence water velocity over the bed increased, distribution became less homogeneous as ammocoetes were found to be more numerous along the bank of the stream and on the upstream and downstream edges of the bed where water velocities were least. In flood ammocoetes were confined to these regions of low velocity and appeared to be concentrated there (Fig. 49).

One other area further down Venison Creek in Concession #5 of South Walsingham Township has also been observed repeatedly. This area, shown in Figure 50, contained two ammocoete beds. Bed "A" had an average depth of water over it of about 6 inches and only a very slight current flowed over it of <0.1 foot per second at average flow. It was composed of very soft mud and organic detritus. One detailed analysis of bed "A" (3 Sept. 1958) showed an average compactness of 600 grams and a preponderance of organic matter in the bed. All mineral matter present passed through sieve #60 and therefore had a particle size of <0.25 millimeter; 16.5% passed sieve #200, thus having a particle size of <0.074 millimeter. Bed "B" was rather similar to that at Concession #8 discussed above. Average water depth over the bed was 6 inches and flow 0.5 foot per second. This bed was composed of sand

with only a very slight admixture of organic matter. Bed "A" has been shown to be of very constant nature, remaining in a fairly constant state from 1957 to 1961. Bed "B", on the other hand, has been frequently washed out in floods and subsequently rebuilt. Ammocoete population density in Bed "A" was generally ten times that in Bed "B".

f) Migration of Ammocoetes

1) Stony Creek Weir

The trap weirs in Stony Creek (Fig. 8) were operated from May 9, 1958 until January 20, 1959, with a few minor interruptions. The site of the weirs is indicated in Figure 45.

Although both P. marinus and E. (L.) lamottei adults were captured entering the stream to spawn, only P. marinus ammocoetes were caught moving downstream. However, this is believed to reflect relative abundance rather than migration habits. Table XXIII gives a summary of lamprey movement through the weirs. All the ammocoetes caught were going downstream. A series of 17 dawn and dusk checks of the weirs showed that most migration was by night. Only one ammocoete entered the trap during daylight hours; this was during a flood.

Several authors have suggested correlation of downstream migration with flood conditions. However, this data showed very poor correlation with water flow, as shown in Table XXIV.

The correlation coefficient "r" for a comparison of ammocoete capture in Stony Creek and mean monthly flow in North Creek (see subsection b of this section) was $r = +0.349$ (necessary value for significance at 5% level 0.707).

A similar correlation with mean temperature gave an "r" value of +0.204. Since temperature and flow are independent, it was considered that a multiple regression using this same data might be profitable. The resultant multiple correlation coefficient "R" was +0.978 (necessary value for significance at the 1% level 0.874). The equation describing this relationship is:

$$Y = 8.21 X_1 + 1.47 X_2 - 125.4$$

where Y = Monthly catch of P. marinus.

X_1 = Mean monthly flow cfs.

X_2 = Mean monthly water temperature °F.

Thus it is concluded that ammocoete migration in Stony Creek was correlated directly with two variables, water temperature and water flow.

Migrating ammocoetes varied in length from 33 millimeters to 164

millimeters and were thus representative of all year-classes (see Figure 39). The preponderance of ammocoetes over 70 millimeters in length is considered to reflect relative size of year groups rather than differences in migration habits.

ii) Reshocking Studies

A second approach to the study of migration in ammocoetes was taken in Venison Creek where an area in the 8th Concession of North Walsingham Township was repeatedly shocked out and the number of ammocoetes of each species caught was recorded. This area, whose position is shown in Figure 45 and which is shown in detail in Figure 48 (ammocoete bed), constituted typical ammocoete habitat in the middle course of Venison Creek. It lay about 3 miles below the lowest spawning grounds of P. marinus (see Fig. 45).

It is considered that these results obtained by reshocking to determine immigration into an ammocoete bed is not such a reliable index of the number of ammocoetes migrating as is a check weir. Bias is inevitably introduced as shocking efficiency is greatly reduced in the turbid water conditions associated with above average flow. Migration at high water is also underestimated due to increased water velocity over part of the bed, rendering it unsuitable habitat. Additionally, since Venison Creek was further from Delhi than Stony Creek weirs, correlation between actual flow from North Creek at Delhi, which was used, is probably less exact than at Stony Creek. In Table XXV, which summarizes monthly ammocoete catches at the station and flow (North Creek) and temperature data, a second index of stream flow, calculated source of run-off is included. This index is equivalent to the amount of precipitation in a given month which does not remain on the ground as snow, plus any snowfall from the previous month melting in the following month.

Table XXVI gives correlation coefficients, both simple and multiple, for comparisons of the number of ammocoetes caught with water temperature, flow and source of run-off. The best correlations are those of the number of ammocoetes caught with water temperature, both of which are significant at the 1% level. It is notable that while comparison with flow gave negative coefficients, that with source of run-off gave positive ones. However, none of these comparisons was significant at the 1% level and only one at the 5% level. Multiple correlation coefficients were in all cases less significant than the simple correlations with temperature.

The relationships between the number of ammocoetes captured and water temperature is shown in Figure 51. It is evident that the points do not fit a straight line. Data for P. marinus appears exponential in character and this is borne out by the fact that log number P. marinus caught plotted against temperature is much closer to a straight line than the original data ($r = 0.89$). However, it is evident that in the case of E. (L.) lamottei the curve rises with temperature only so far, then falls. Although the data for P. marinus do not show this fall so clearly, there is some evidence of a decline in numbers immigrating with this species also. It appears that maximum immigration of E. (L.) lamottei occurred at about 54°F and maximum immigration of P. marinus at about 57°F.

iii) Information Obtained from General and Detailed Distribution Studies

The observed distribution of ammocoetes during the general survey gave some information concerning migration.

Sea lamprey ammocoetes were found only below known spawning grounds, indicating that upstream migration did not take place. The discovery of a few P. marinus ammocoetes at the mouths of tributary streams having no spawning did indicate very short migrations or movement against weak current. Although the wider distribution of spawning facilities of E. (L.) lamottei makes similar information more difficult to obtain for this species, conclusions were in general the same as for P. marinus.

The distribution of age classes of ammocoetes within the stream in relation to the location of spawning grounds gives information concerning the rate of migration.

Sea lamprey ammocoetes which were in the process of transformation have been found in suitable substrata up to the highest spawning ground, and the same was true of American brook lampreys. Thus, evidently some individuals move downstream little, if at all, during their lifetimes. It is evident, however, that most ammocoetes move steadily downstream. In Venison Creek sufficient samples have been taken to be able to plot the average movement of year-classes downstream. Data is better for P. marinus, as its spawning grounds are more localized than those of E. (L.) lamottei.

At a station in Concession #12, N. Walsingham Township, about 1/2 mile below the lowest known spawning grounds of P. marinus, young-of-the-year of both P. marinus and E. (L.) lamottei were found to be present by mid-August (eggs hatch about June 1, on the average), and by October were as numerous as those one year older. From October to the following August, 0+ specimens were most numerous. At the Concession #8 re-shocking area, young-of-the-year of both species were present by the first week in September; 1+ specimens of both species, however, were usually the most numerous at the Concession #8 area. About one mile further downstream, however, 2+ animals of both species were dominant. At an area repeatedly checked in Concession #5, young-of-the-year were also found in September, but only in very small numbers; 3+ animals of both species were the most numerous. Table XXVII summarizes this data and gives the approximate distance of each sampling station below the lowest known sea lamprey spawning station. This data indicates that in Venison Creek most ammocoetes move downstream at about 2 to 2 1/2 miles per year.

In other collections made in Venison Creek containing smaller numbers of specimens, but made in many more locations than those described above, similar results were obtained. Stations less than 4 miles from the lowest P. marinus spawning grounds were generally dominated by young-of-the-year and one-year-plus specimens of both species. At between 4 and 6.5 miles downstream, most stations had mostly 2+ animals and between 7 and 7.6

miles most individuals of both species collected were 3+ years old. Most of these collections were made from July to September and thus specimens were about 1 to 4 months past a whole year in age. Thus, these data too would indicate a mean migration distance of 2 and 2½ miles per year.

It should be pointed out that the distances mentioned are those measured on a 4" = 1 mile scale map. Actual distance by stream must be greater than this and probably is about 1½ times greater.

iv) Observed Ammocoete Swimming Behaviour

Many ammocoetes have been observed when swimming after they have left the bottom in response to an electric shock. In general, it was observed that they would orientate with their heads upstream; however, swimming was invariably so weak that they were swept downstream, except at water velocities less than 0.5 foot per second. Some ammocoetes, however, showed no orientation to current and swam haphazardly. All disturbed ammocoetes sought the bottom within about 30 feet of where they left it and much nearer in very slack water.

g) Ammocoetes as Members of the Stream Community

No detailed study was conducted of this phase of ammocoete biology in Big Creek. In Venison Creek observation and collection indicated that ammocoetes were the most abundant fish. Species commonly found in similar habitat were Cottus bairdi, Etheostoma nigrum and Rhinichthys atratulus.

EXPERIMENTAL STUDIES

Experimental studies on the biology of sea lamprey larvae have been limited to topics which were of importance in explaining phenomena observed in the field.

a) Circadian Rhythm of Free-swimming Activity

Apart from observations by Enequist (1937) on nocturnal free-swimming activity in ammocoetes, there is no data on circadian activity rhythms.

Experiments were conducted in an artificial stream using two lighting cycles, 12 hours on and 12 hours off and 18 hours on and 6 hours off at 50°F ± 1°F; and one lighting cycle, 18 hours on and 6 hours off at 60°F ± 1°F. Each experiment lasted three to four weeks. Fifteen P. marinus caught three days before the first experiment began were used for the entire test. Experimental animals were allowed two to seven days to settle down and thermally acclimate before activity recordings were begun. Occasional feeding from green water cultures was provided. Activity was recorded both as the number of contacts with the sensors and as the number of periods of repeated contacts per hour.

The results of the first experiment at 50°F ± 1°F, with the 12 hours

on 12 hours off lighting cycle, are shown in Table XXVIII; for the second experiment at $50^{\circ}\text{F} \pm 1^{\circ}\text{F}$, 18 hours on 6 hours off, in Table XXIX; and for the third experiment at $60^{\circ}\text{F} \pm 1^{\circ}\text{F}$, 18 hours on 6 hours off, in Table XXX.

Table XLII summarizes results for the series of experiments. Throughout the experiments there was a clear circadian rhythm. Almost all activity occurred during the hours of darkness and was at a maximum during the second hour. There was some indication of a second period of activity later; this occurred in the eighth hour of darkness in the 12-hour-off cycle and in the fourth to sixth hours in the 6-hour cycle. Reducing the hours of darkness had the effect of compressing the total period of activity to five or six hours from eight hours. Little or no activity took place for the last four hours of the 12-hour cycle or for the last hour of the 6-hour darkness cycle.

As shown in Table XLI, activity was more intense at 60°F than at 50°F . It does, however, seem clear that at both temperatures ammocoetes did not swim actively each night, since on many nights no activity at all was recorded.

b) Activity Within the Burrows

Photographic exposures of ammocoete burrow mouths made during the hours of darkness in the experiments described above showed that no part of the ammocoete's body was visible at any time.

Mapping of the positions of the mouths of burrows twice a day showed that burrows were of a temporary nature and normally lasted less than 24 hours. New burrows were made from within the sand, both during darkness and during illumination. There was no evidence to indicate any circadian rhythm of burrow construction. Experiments using fluorescein dye in 5% aqueous solution as a water marker indicated that a continuous current was normally drawn into ammocoete burrows. However, ammocoetes occasionally reacted to the dye by giving a sharp reversed expiration immediately followed by a normal inflow of water. On one occasion complete reversal of the direction of flow of water in the burrow was observed.

Observations made in the thin observation tanks at about 55°F showed that the burrows of ammocoetes were variable in length. Distances on the surface of the sand between the head and tail of the burrow varied from 30 millimeters to 250 millimeters. The burrows were usually less than 50 millimeters below the surface at the deepest part. Ammocoetes took up a variety of positions in their burrows, some lying with the head a few millimeters below the head hole, others with their tails a similar distance from the other end. In long burrows ammocoetes were observed to lie with their heads up to 140 millimeters from the head hole. There was no fixed orientation of the burrows with respect to the direction of water flow.

c) Swimming Speed

Only preliminary experiments on this subject have been carried out. Using *P. marinus*, 100 spontaneous swimming-speed measurements and 71 maximum (after stimulus) swimming speed trials were carried out on 10

specimens at 4°-7°C (acclimation temperature 4°C). The ammocoetes ranged in size from 31 millimeters to 140 millimeters. Using E. (L.) lamottei, 28 spontaneous speed trials and 27 maximum speed trials were carried out between 5°C and 7°C (acclimation at 4°C) with 4 specimens ranging from 54 to 128 millimeters. At 10°C (acclimation 10°C), 16 spontaneous and 7 maximum swimming speeds were measured using 2 animals, 176 millimeters and 108 millimeters in length.

During all these trials, experiments were discontinued as soon as each specimen showed signs of fatigue. The results are shown in Table XLIII. It is notable that there was, as expected, a general increase of swimming speed with size; the quantity: swimming velocity/ $\sqrt{\text{length}}$, was almost a constant averaging 0.028 for spontaneous swimming speed of P. marinus at 4°-7°C and 0.061 for maximum swimming speed. For E. (L.) lamottei under similar conditions the two means were 0.019 and 0.040 respectively. At 10°C insufficient results to calculate means were obtained. It must be emphasized that these results are too scanty to form a basis for conclusions on the swimming speeds of ammocoetes. They do, however, indicate that swimming speeds are in general rather slow and that E. (L.) lamottei does not swim as fast in proportion to its length as P. marinus.

DISCUSSION

Many workers, starting with Müller (1856), have attempted to determine the length of the ammocoete period in lampreys. So far no method of aging other than by length-frequency determinations has been discovered. The length-frequency method has proved to be far from ideal, since large variations in growth rate occur between individuals of the same age, both within streams and from stream to stream. Consequently, the recognition of age groups after the first two years of life is invariably difficult. As discussed in the literature review (page 6), some authors have been unable to estimate length of larval life in ammocoete populations, others have based estimates on insufficient material and others have given different interpretations to the same material. As shown in Table IV, estimates of the length of larval life have varied widely. Recently, however, Hardisty (1961) has published information on the rate of growth and length of larval life of P. marinus, L. planeri, and L. fluviatilis, which has aided the determination of length of larval life. Hardisty demonstrated that in his material the growth rate was almost linear up to the start of transformation. It was shown that in P. marinus and E. (L.) lamottei in Venison Creek growth was also linear as far as it could be confidently determined. Extrapolations of the growth line to transformation size gave a probable length of larval life of P. marinus of 5½ years and E. (L.) lamottei of 4½ years. The estimate for P. marinus agrees with that of Hardisty (1961) also for specimens from the Great Lakes watershed and with that of MacDonald (1959) for British P. marinus. The estimate for E. (L.) lamottei agrees with those of Hubbs (1924) and Okkelberg (1921). The estimates were based on the assumption that metamorphosis takes place as soon as the ammocoete reaches suitable size; if a one-year rest period occurs before metamorphosis, as was suggested by Gage (1928) and considered as possible by Applegate (1950), one year should

be added to each estimate. It must also be remembered that these estimates are based on a linear rate of growth up to metamorphosis; Hubbs (1924) showed that growth in E. (L.) lamottei was a little increased in the final year of larval life. Such an increase, however, would not be sufficient to reduce length of larval life by one year, even if it occurred in Venison Creek.

The estimates refer only to the average ammocoetes of each age group. The variation in the rate of growth of larvae is such that it is considered probable that limits of -2 and +4 years must be placed on the estimate for the period of transformation of an entire age class of P. marinus and -2 and +3 years for E. (L.) lamottei.

Hardisty (1961) found that the annual cycle of growth he found in L. planeri could be correlated with the density of phytoplankton, growth being most rapid when phytoplankton was most abundant. It is assumed that the growth cycle observed in both P. marinus and E. (L.) lamottei in Venison Creek was also caused by fluctuation in the amount of food. No accounts of similar winter shrinkage to that found in Venison Creek appear in the literature, although several others report cessation of growth in winter (Hardisty, 1944; Schultz, 1930).

In general the broad or, as it has been termed in this report, the macro-distribution of ammocoetes and their migration are closely bound together. One aspect of distribution, however, that of their maximum spread up a stream, is considered to be a function of the spawning requirements of the adult lampreys. Some authors (Stauffer and Hansen, 1958; Bams, 1958) state that ammocoetes were rare or absent in very small streams. Size of stream would, however, not seem a limiting factor to larval lampreys since they can be kept easily in small tanks of still or running water. In addition, in Big Creek larvae of both species were found in very small streams, down to about 1 foot in width and well below 1 cubic foot per second in flow.

There are many conflicting reports in the literature concerning the extent of distribution of lamprey ammocoetes below spawning grounds; in some locations ammocoetes were concentrated in relatively short reaches below the spawning grounds (Schultz, 1930; Leach, 1940), in other streams wide distribution of ammocoetes downstream was observed (Enequist, 1937; Applegate, 1950). However, as pointed out by Schultz (1930), Leach (1940) and Enequist (1937), these broad distribution characteristics appear to be correlated with the nature of the streams. Little work has been carried out on the factors affecting migration; but Applegate (1961) showed that it was affected by stream flow. For migration to take place at all, natural free-swimming activity of ammocoetes must take place. Enequist (1937) showed that some free-swimming activity took place at night. In the present study it was found that in Stony Creek almost all downstream migration was nocturnal. These results were confirmed by laboratory experiments which showed that free-swimming activity was again almost entirely nocturnal, having a peak in the second hour of darkness with some evidence for a second smaller activity peak later in the night. It is interesting to

note that a similar pattern of activity has been observed in sea lampreys during their spring spawning run (Lamsa, 1957; McCauley, 1958). It must be during this nocturnal activity that downstream migration takes place. It seems fairly clear that the migration is not a very active one. According to Enequist (1937), active larvae swam haphazardly in relation to the current, except when they were in contact with the bottom when they would swim against the current. Several authors have noted that ammocoetes disturbed during daylight have shown little directional movement. Applegate (1950) reported that such ammocoetes swam aimlessly with the current, and Bams (1958) made similar observations. During this study, ammocoetes have been observed to swim in all directions during daylight after being disturbed. It was observed, however, that the majority of ammocoetes orientated facing upstream, but swam rather weakly and were carried downstream, except in very slow water. Experiments on swimming speed in ammocoetes showed that normal swimming speeds were slow and, although data on this point is far from complete, it would appear that few ammocoetes could breast water velocities of over 1 foot per second for long. Unpublished work by Sholdice (1962) suggests that an ammocoete six inches in length could swim at about 18 inches per second for one minute (20°C). No ammocoetes could swim at more than four body lengths per second for more than 20 seconds. We therefore get a picture of ammocoetes leaving the bottom at night and in many localities being swept downstream because of their rather feeble swimming activities. These facts explain many of the observed patterns of distribution of ammocoetes in streams. In streams of a fairly constant, slow flow, ammocoetes emerging from the bottom would be able to reburrow close to their original location. In exceptionally slow reaches, some upstream progress could be made by some individuals. However, in faster streams or at times of flood in normally slow streams, many emerging ammocoetes would meet or swim into faster water than they could maintain their position against. Such specimens would be transported downstream. Ammocoetes being carried downstream would be unable to enter the bottom until they reached water so slow that they could maintain position and, in addition, produce the necessary force to drive their heads into the bottom. Thus, after floods the limited distribution of ammocoetes in the slackest water is explained. The laboratory experiments showed that free swimming activity was not a universal nightly occurrence. Indeed, it seemed probable that even at temperatures where optimum activity took place, only an occasional ammocoete would emerge at night. At reduced temperatures activity would also be reduced. It is possible that some ammocoetes never leave the mud at all, since full grown ammocoetes may be found among the spawning beds. It is realized that small areas of negligible water movement do occur even in the gravel riffles characteristic of spawning locations; these areas are usually so limited in size, however, that a randomly-swimming ammocoete would soon encounter water beyond its swimming ability. Studies on migration and immigration in Stony Creek and Venison Creek both showed that temperature played a part in migration; however, the effect was more pronounced in Venison Creek where temperature was found to be the main factor controlling immigration into the test area. In Stony Creek water flow appeared equally important to temperature. Applegate (1961) showed that in a stream in Michigan flow appeared to be the factor controlling migration. It is probable that in all these cases both flow and temperature enter into the migratory

pattern, but the results are biased in various ways, except in the case of the Stony Creek weir. In Venison Creek rise in water level caused turbidity, which, combined with the increased water depth, made efficient shocking impossible; in addition, during flood conditions water velocity over part of the bed increased so that it was probably unusable as larval habitat. Thus, the effect of high water on migration was under-estimated. In the case of the stream described by Applegate (1961), the method of capture was by means of a "wolf" trap, which is essentially a dam over the top of which the water flows, subsequently dropping down through a screen. Above the weir a deep, fairly still pool is formed. During normal flow conditions this pool probably acts as a collecting basin for migrating ammocoetes. Only at times of flood would flow be great enough to carry many specimens over the weir.

In Venison Creek, results indicated that maximum immigration activity occurred at a mean temperature of about 57°F for *P. marinus* and 54°F for *E. (L.) lamottei*. Applegate (1950) showed that peak spawning migrations in sea lampreys occurred between 50°F and 65°F. Skidmore (1959) similarly showed a peak spawning migration of sea lampreys at 55°F, but considered that activity was also linked with temperature rise. Insufficient data on ammocoete migration is available to see if a parallel exists in this respect too. No data is available on spawning migration activity in the American brook lampreys.

In natural conditions maximum rate of downstream movement of ammocoetes would be expected in fast reaches. In slow reaches below fast ones, ammocoetes would tend to build up and migrate little.

It is hard to believe, however, that migration can be strictly a passive movement. Evidence collected in Lake Superior showed that many ammocoetes passed the typical slow, silty, lower reaches of rivers and streams and reached the lake. Once in the lake, ammocoetes moved far from the river mouth. Although lake currents undoubtedly aid dispersal, these are generally very slow compared to those of rivers and streams, and it is believed that some active migration must take place.

In regard to the finer distribution of ammocoetes within that part of streams where they occur, a great variety of information has been published. All authors agree that ammocoetes are most abundant in silt; many point out that such deposits were found in depressions of the stream bed, on the inside of stream bends, behind obstructions, etc. (Reighard and Cummins, 1916; Schultz, 1930; Applegate, 1950; Hardisty, 1944; Maskell, 1929). However, it is believed that all these situations can be described in terms of two parameters, bottom hardness and water velocity. It was shown in Venison Creek that population density of ammocoetes was proportional to these, being greatest in soft bottoms with slow flow. Such conditions occur in places where ammocoetes have been found to be concentrated. In regard to the formation of what have become known as ammocoete beds, which are areas of suitable bottoms among less suitable habitat, these would only be found where the mean stream velocity exceeds that required for the laying down of silt beds. Below such a velocity ammocoete beds as such do not occur, since all the stream bed is suitable habitat. Several authors have stated that ammocoetes

are more common in, or even preferred, shallow water (Churchill, 1945; Bams, 1958). From the work on Venison Creek it is believed that this is only true in places where the mean water velocity is just over the critical level for silt deposition and where at the side of the stream the velocity falls below this level due to friction. Retardation of water at the bottom and sides of streams is a general rule. The statement by Schroll (1959) that surface water velocity over ammocoete burrows was 2.07 feet per second would appear incorrect, in that soft bottoms cannot be formed at such water velocities.

The work on Venison Creek suggests that certain limits can be laid down in terms of bottom hardness and water velocity for ammocoete burrowing. Using the multiple regression equation for P. marinus and substituting zero for population density and then in turn velocity and compactness, the figures 2.04 feet per second and 2224 grams respectively are given; for E. (L.) lamottei the corresponding figures are 2.6 feet per second and 2691 grams. With what is known of swimming speed, the water velocity limits appear realistic, since no ammocoete could burrow into an infinitely soft bottom if it could not breast the current over it.

The surveys in Lake Superior (MS 710) have, however, shown the danger of assuming ammocoetes will not be present because the bottom is unsuitable. The above limits may well apply to the construction of normal burrows, but where the bottom is too hard ammocoetes were found to take advantage of almost any existing cover. They were found in the interstices of stones, in gravel, under wood, old tires and other debris, and in very small pockets of soft sediment among rocks.

Perhaps the most important knowledge gained through these surveys is of a very general nature. We must realize that lampreys are a highly adaptable group of animals and that it is dangerous to draw any conclusions that are based on only limited observation or research. This adaptability applies to the entire life cycle of the sea lampreys and probably to other species as well; in the larval stage it is well exemplified by the range of habitat utilized and in the adult stage by its wide tolerance of spawning conditions.

CONCLUSIONS

- i) In Venison Creek ammocoetes of P. marinus and E. (L.) lamottei grow only during the warmer months. Both species show some shrinkage during the winter.
- ii) Length of the larval period was $5\frac{1}{2}$ years for the average P. marinus and $4\frac{1}{2}$ years for the average E. (L.) lamottei.
- iii) Ammocoetes were widely distributed in soft bottoms below spawning sites in Big Creek.
- iv) Ammocoetes were most abundant where the current was very slow

and the bottom very soft. No other factors controlling detailed distribution were found.

v) In the absence of good bottom conditions, ammocoetes were able to find shelter in almost all naturally-occurring bottom materials.

vi) Ammocoete migration was almost entirely downstream and nocturnal. The rate of migrational activity was governed both by water flow and by temperature. Speed of migration was considered to be a function of stream gradient.

vii) P. marinus and E. (L.) lamottei were found to exhibit similar requirements for larval habitat and to migrate in the same manner. Distribution was similar. The only striking difference observed was the faster rate of growth and shorter larval period in E. (L.) lamottei.

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NOTES - TABLES X, XI, XII, XIII AND XIV

- 1) One inch of snow is taken to be the equivalent of one inch of rain.
- 2) Total source of run off (total source R.O.) is calculated as

follows:

Total precipitation plus rainfall equivalent of snow
remaining from the previous month minus rainfall
equivalent of snow remaining at the end of the month.

Table I. Distribution of ammocoetes in relation to stream bottom types as reported in the literature.

Author, date	Species	Soft mud/silt	Silt/ sand	Silt/ debris	Sand	Gravel	Weed beds	Stiff muck
Reighard, Cummins, 1916	<u>I. fossor</u>	...	++++	...	+	+	...	0
Maskell, 1929	<u>G. australis</u>	++	++	++	++	+	...	...
Schultz, 1930	<u>L. planeri</u>	...	++++	+++	+	0	+	0
Hardisty, 1944	<u>L. planeri</u>	+++	+++	++++	+	+	...	...
Churchill, 1947	<u>L. fossor</u>	0	++++	...	0	...	++++	...
Applegate, 1950	<u>P. marinus</u>	+++	++++	++++	+	+	++++	...

Key: ++++ very abundant

+++ abundant

++ common

+ rare

0 absent

Table II. Burrowing depth in relation to size of P. marinus ammocoetes from Applegate (1950).

Ammocoete length (mm)	Burrow depth (mm)
20	<13 mm.
31-41	<33 mm, usually 19-26 mm.
50-90	usually 51-75 mm.
100-160	usually up to 125 mm, but up to 150 mm in very soft bottoms.

Table III. Maximum population densities of larval lampreys cited by various authors.

Author, date	Species	No. of larvae	Area (sq. ft)	Ammocoetes per sq. ft.
Reighard & Cummins, 1916	<u>I. fossor</u>	61	50.0	1.21
Schultz, 1930	<u>L. planeri</u>	170	4.7	36.6
Churchill, 1947	<u>I. fossor</u>	153	169.0	0.9
Applegate, 1950	<u>P. marinus</u> ^a	630	226.0	2.8
Applegate, 1950	<u>P. marinus</u> ^b	...	226.0	Ave. 14.0
Applegate, 1950	<u>P. marinus</u> ^c	...	226.0	Ave. 16.8

^aOlder than young-of-the-year.

^bYoung-of-the-year.

^cAll ages.

Table IV. Estimates of the duration of the larval period in years, in various species of lampreys by various authors.

Author	P.m.	L.p.	L.f.	L.d.	L.a.	E.l.	L.f.
Hardisty, 1961	5½	5½	5½	...	...	...	...
Macdonald, 1959	5½	4½	5½	...	...	...	...
Seversmith, 1953	...	...	...	...	3	...	...
Zanandrea, 1951	...	4½	...	...	...	...	...
Applegate, 1950	4	...	...	...	...	...	...
Hardisty, 1944	...	4½	...	...	...	...	...
Knowles, 1941	...	2-3	...	...	...	...	...
Leach, 1940	...	...	...	...	...	...	6
Chappuis, 1939	...	...	...	3½	...	...	...
Ivanovna-Berg, 1931	...	4	...	...	...	...	...
Schultz, 1930	...	3½	...	...	...	...	...
Hubbs, 1924	...	...	...	...	...	4½	...
Okkelberg, 1922	...	...	...	...	...	...	6½
Okkelberg, 1921	...	...	...	...	...	4½	...
Wigley, 1959	7	...	...	...	...	...	...

Legend: P.m. = Petromyzon marinus.
L.p. = Lampetra planeri.
L.f. = Lampetra fluviatilis.
L.d. = Lampetra danfordi.
L.a. = Lampetra aepyptera.
E.l. = Entosphenus (L.) lamottei.
L.f. = Ichthyomyzon fossor.

Table V. Myomere counts of Ontario lampreys.

Species	No. of specimens	No. of trunk myomeres	
		Range	Average
<u>L. unicuspis</u>	138	27-55	50.7
<u>L. fossor</u>	150	51-58	53.5
<u>E. (L.) lamottei</u>	154	64-70	67.5
<u>P. marinus</u>	131	67-74	70.1

(From Vladykov, 1949)

Table VI. U.S. standard sieve series mesh sizes.

Number	Mesh size inches	Mesh size millimeters
4	0.187	4.76
6	0.132	3.36
8	0.0937	2.38
18	0.0394	1.00
30	0.0232	0.59
60	0.0098	0.25
200	0.0029	0.074

Table VII. Main characteristics of Big Creek and its major tributaries.

Location	Elevation	Distance	Drop	Gradient
<u>Big Creek</u>				
Source	950'			
Delhi	700'	27.8 miles	250'	9.0 ft/mile
Venison Cr. Mouth	575'	19.2 miles	125'	6.5 ft/mile
Mouth	572'	7.5 miles	3'	0.4 ft/mile
<u>Venison Creek</u>				
Source	750'			
Dam	715'	4.1 miles	35'	8.5 ft/mile
Con. x rd.	625'	4.6 miles	90'	19.5 ft/mile
Mouth	575'	5.5 miles	50'	9.1 ft/mile
<u>North Creek, North Branch</u>				
Source	800'			
Mouth	700'	5.0 miles	100'	20.0 ft/mile
<u>North Creek, South Branch</u>				
Source	775'			
Mouth	700'	6.0 miles	75'	12.5 ft/mile
<u>Stony Creek</u>				
Source	800'			
Mouth	675'	7.7 miles	125'	16.2 ft/mile

Table VIII. Mean monthly resistivities and monthly resistivity ranges in Stony Creek.

Year	Month	Resistivity	Resistivity Range	No. of readings
		Ω/cm^3 at 20°C		
1958	May	2580	2460-2660	17
	June	2570	2470-2630	16
	July	2640	2470-2800	20
	Aug.	2430	1690-2750	28
	Sept.	2240	1850-2560	26
	Oct.	2230	1950-2480	27
	Nov.	2070	1430-2500	25
	Dec.	2070	1840-2410	22
1959	Jan.*	2160	2000-2710	20
	Feb.	...	...	1
	Mar.	3010	2460-3390	7
	Apr.	2760	2240-3520	5
Mean		2160		

*In January 1959 flooding over ice caused abnormally resistive water conditions with readings up to 7,790 Ω/cm^3 . These readings are not included.

Table IX. Mean monthly resistivities and monthly resistivity ranges in Venison Creek.

Year	Month	Resistivity	Resistivity Range	No. of readings
		Ω/cm^3 at 20°C		
1958	May	2700	2610-2840	10
	June	2690	2620-2735	3
	July	2760	2530-2970	11
	Aug.	2670	2430-2970	17
	Sept.	2460	2350-2580	6
	Oct.	2570	2280-2760	5
	Nov.	2730	2500-2710	2
	Dec.	...	...	1
1959	Jan.*	2490	2180-2790	8
	Feb.	...	...	1
	Mar.	3240	2460-3390	6
	Apr.	2680	2240-3520	4
Mean		2700		

*In January 1959 flooding over ice caused abnormally resistive water conditions with readings up to 10,450 Ω/cm^3 . These readings are not included.

Table X. Summary of weather reports from Delhi - 1957.

Month	Temperature (°F)			Precipitation (inches)			Total source R.O.
	Mean Max.	Mean Min.	Mean	Rain	Snow	Total ppt.	
Jan.	23.84	11.06	17.45	1.63	19.25	3.56	3.36
Feb.	34.54	18.16	26.85	0.91	15.50	2.46	2.66
Mar.	41.98	26.63	34.30	1.99	6.00	2.59	2.59
Apr.	55.65	36.88	46.26	3.22	11.00	4.34	4.34
May	64.23	43.66	53.95	3.91	...	3.91	3.91
Jun.	78.18	56.65	67.42	4.74	...	4.74	4.74
Jul.	79.62	56.63	68.13	3.25	...	3.25	3.25
Aug.	76.03	53.60	64.81	5.54	...	5.54	5.54
Sep.	70.15	49.77	59.95	5.19	...	5.19	5.19
Oct.	58.24	37.32	47.78	3.36	...	3.36	3.36
Nov.	45.88	32.97	39.42	2.97	4.00	3.37	3.37
Dec.	37.40	25.91	32.65	4.47	3.50	4.82	4.67
						46.13	

Table XI. Summary of weather reports from Delhi - 1958.

Month	Temperature (°F)		Precipitation (inches)			Total source R.O.
	Mean Max.	Mean Min.	Mean	Rain	Snow	Total ppt.
Jan.	29.47	18.85	24.16	0.34	14.00	1.74
Feb.	25.00	11.25	18.12	0.64	11.00	1.74
Mar.	37.90	27.53	32.62	0.06	5.00	0.56
Apr.	58.47	34.80	46.64	2.47	1.00	2.57
May	67.26	40.16	53.71	1.91	...	1.91
Jun.	71.53	48.07	59.80	4.19	...	4.19
Jul.	79.70	59.80	69.80	2.26	...	2.26
Aug.	79.32	54.45	66.94	2.07	...	2.07
Sep.	70.13	51.77	60.90	3.37	...	3.37
Oct.	59.71	41.45	50.58	1.14	...	1.14
Nov.	46.33	32.37	39.35	1.52	11.00	2.62
Dec.	26.26	10.45	18.85	0.09	5.00	0.59
						24.76

Table XII. Summary of weather reports from Delhi - 1959.

Month	Temperature (°F)		Precipitation (inches)			Total source R.O.
	Mean Max.	Mean Min.	Mean	Rain	Snow	Total ppt.
Jan.	25.74	12.77	19.26	1.07	2.37	3.44
Feb.	28.93	14.68	21.81	2.27	8.50	3.12
Mar.	37.42	21.84	29.63	1.37	13.25	2.71
Apr.	56.20	34.63	45.42	3.81	...	3.81
May	69.11	46.22	57.67	4.09	...	4.09
Jun.	77.87	54.10	65.98	0.94	...	0.94
Jul.	83.81	57.58	70.69	1.98	...	1.98
Aug.	83.61	63.65	73.63	6.23	...	6.23
Sep.	75.40	54.20	64.80	2.55	...	2.55
Oct.	56.52	42.74	49.63	4.34	...	4.34
Nov.	40.53	29.16	34.84	2.66	6.75	3.34
Dec.	33.45	24.27	28.86	3.47	1.50	3.52
						40.17

Table XIII. Summary of weather reports from Delhi - 1960.

Month	Temperature (°F)		Precipitation (inches)			Total source R.O.
	Mean Max.	Mean Min.	Mean	Rain	Snow	Total ppt.
Jan.	29.13	19.84	24.49	2.19	12.00	3.39
Feb.	29.00	18.45	23.73	1.70	9.50	2.65
Mar.	28.90	10.65	19.78	1.26	20.00	3.26
Apr.	55.47	36.60	46.04	4.48	...	4.48
May	63.48	47.06	55.27	3.48	...	3.48
Jun.	75.93	51.87	63.90	3.72	...	3.72
Jul.	78.90	53.90	66.40	1.78	...	1.78
Aug.	78.77	54.68	66.73	2.69	...	2.69
Sep.	74.20	52.60	63.40	0.69	...	0.69
Oct.	60.51	36.84	48.67	2.13	...	2.13
Nov.	48.57	33.80	41.18	2.39	...	2.39
Dec.	28.10	15.90	22.00	0.13	17.00	1.83
						32.49

Table XIV. Summary of weather reports from Delhi - 1961.

Month	Temperature (°F.)		Precipitation (inches)			Total source R.O.
	Mean Max.	Mean Min.	Mean	Rain	Snow	Total ppt.
Jan.	23.97	10.03	17.00	0.00	8.00	0.80
Feb.	32.57	15.82	24.19	1.50	11.00	2.60
Mar.	40.10	26.80	33.50	3.17	1.00	3.27
Apr.	46.70	32.10	39.40	5.58	2.00	5.78
May	62.50	41.00	51.80	3.05	...	3.05
Jun.	72.80	51.90	62.40	3.57	...	3.57
Jul.	80.00	59.00	70.00	2.04	...	2.04
Aug.	76.90	57.80	67.40	5.81	...	5.81
Sep.	75.10	55.30	65.20	2.29	...	2.29
Oct.	62.00	42.60	52.30	0.38	...	0.38
Nov.	45.20	30.30	37.80	2.87	3.00	3.17
Dec.	32.40	21.40	26.90	2.05	5.00	2.25
						35.31

Table XV. Summary of comparable temperature data for air temperatures at Delhi and water temperatures in Venison Creek and Stony Creek, 1958. (Monthly means °F.)

Month	Air temp. at Delhi, °F.	Water temp. at Stony Cr., °F.	Water temp. at Venison Cr., °F.
July	69.8	64.2	...
Aug.	66.9	61.2	58.1
Sep.	60.9	56.1	55.0
Oct.	50.6	47.7	49.1
Nov.	39.4	39.9	43.5
Dec.	18.8	32.2	35.2

Table XVI. Calculated mean monthly water temperatures in Stony and Venison Creeks, 1957 to 1961.

Month	Stony Creek	Venison Creek
Jan.	32.0	35.5
Feb.	32.0	36.5
Mar.	32.0	40.0
Apr.	43.2	47.0
May	51.7	51.8
Jun.	58.8	56.1
Jul.	63.0	58.6
Aug.	62.0	58.0
Sep.	58.0	55.6
Oct.	47.7	49.5
Nov.	38.6	44.0
Dec.	32.0	37.9

Annual Total	16859.4	17428.9
Annual Mean	46.2	47.8

Table XVII. Mean monthly discharge in Big Creek and North Creek, 1957-1961, in second feet.

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Max.	Min.	Mean
<u>Big Creek at Delhi</u>															
1957-58	76	133	298	126	98	220	165	69	70	55	39	52	740	15	117
1958-59	61	70	67	124	158	375	252	133	66	27	53	60	783	10	120
1959-60	77	123	178	111	168	286	653	231	112	61	60	43	4910	34	175
1960-61	52	63	54	50	109	146	197	164	100	57	68	45	364	25	92
Mean	66	97	149	103	133	257	317	149	87	50	55	50	1699	21	126
<u>Big Creek at Walsingham</u>															
1957-58	141	250	407	238	172	328	261	141	139	105	77	94	765	60	196
1958-59	94	115	118	211	260	610	439	236	180	75	81	99	828	60	209
1959-60	162	197	296	257	274	307	840	432	213	135	128	117	3060	99	279
1960-61	105	110	95	87	148	263	361	245	160	105	112	99	617	93	157
Mean	126	168	229	198	213	377	475	264	173	105	100	102	1318	78	210
<u>North Creek at Delhi</u>															
1957-58	15.0	29.0	41.0	17.0	15.0	30.0	22.0	10.0	10.0	9.0	6.0	7.0	127	3.0	18
1958-59	7.0	10.0	9.9	17.9	19.9	41.5	33.2	20.2	12.0	6.5	5.6	7.4	119	2.0	16
1959-60	10.5	17.1	26.1	21.0	27.1	58.0	84.0	36.1	20.9	8.8	9.2	7.2	1000	3.6	27
1960-61	9.5	10.7	7.7	6.5	15.1	27.9	37.6	31.3	19.7	9.0	14.4	10.7	105	4.5	17
Mean	10.7	16.7	21.2	15.6	19.3	39.3	44.2	24.2	15.7	8.3	8.8	8.1	338	3.3	19.5

Table XVIII. Flow measurements and estimates for Big Creek and its major tributaries.

Stream	Flow		
	Mean	Mean Max.	Mean Min.
Big Creek - Teeterville*	50	700	10
" " - Delhi**	126	1699	21
" " - Walsingham**	210	1318	78
" " - mouth*	250	1500	90
Venison Creek - dam*	15	100	8
" " - mouth***	35	150	15
North Creek, north branch - Delhi**	19.5	338	3.3
" " south branch - Delhi*	20	350	4
Stony Creek - mouth*	15	150	4
Cranberry Creek - mouth*	10	100	3
Trout Creek - mouth*	6	75	2

*Estimated data only.

**Full data available.

***Partial data available.

Table XIX. Results of micro-distributional survey - Venison Creek.

Area No.	W.T. °C	S.T. °C	W. Vel. ft/sec	Av. depth in.	W at 18°C	S pH	O ₂ % Satn.	Area. m ²	I.L. factor	Soil Comp.	Soil Type	Miles to Sp.G.	Total P.m. m ²	P.m. Total per m ²	E.l. Total per m ²	Total amm.		
1	18.5	16.0	0.4	21	2350	8.1	...	107	20	0.95	2000	Gravel, sand, clay	...	0	0.00	3	0.15	3
2	18.5	15.0	0.3	4	2750	8.0	...	97	3	0.99	150	Muddy sand	...	0	0.00	0	0.00	12
3	18.5	14.0	1.1	8	2750	8.0	...	97	15	0.86	1100	Sand	...	0	0.00	1	0.07	1
4	16.3	15.5	0.4	8	2680	8.0	7.5	92	6	0.10	800	Muddy sand	...	9	1.50	13	2.17	23
5	16.3	15.8	0.7	6	2680	8.1	7.4	92	10	0.03	1000	Sand	...	0	0.00	2	0.20	2
6	16.3	15.8	0.3	2	2680	8.1	7.4	92	2	0.08	150	Sand	...	8	4.00	8	4.00	18
7	15.5	14.5	1.5	12	2780	7.9	7.8	92	13	0.12	700	Sand	...	...	...	1	0.07	1
8	15.8	14.5	1.0	6	2780	7.9	7.8	92	2.5	0.07	250	Muddy sand	...	3	0.80	1	0.40	15
9	16.2	13.0	1.0	12	2680	7.9	7.2	82	7	0.80	1000	Sand	...	0	0.00	0	0.00	0
10	16.2	14.0	0.9	6	2680	7.9	7.5	82	2	0.90	800	Sand	...	5	2.50	2	1.00	7
11	16.2	12.2	0.5	3	2680	8.2	7.9	93	4	0.01	800	Muddy sand	0.1	2	0.50	10	2.50	28
12	14.3	13.0	1.0	2	2160	7.9	7.8	92	6	0.06	700	Sand	0.5	0	0.00	0	0.00	0
13	16.5	15.0	0.8	3	2200	8.0	7.7	97	8	0.06	1200	Sand	0.5	0	0.00	2	0.25	2
14	17.0	15.0	0.9	10	2220	7.8	7.6	99	12	0.38	600	Sand	0.8	9	1.33	3	0.25	12
15	15.5	13.5	0.9	12	2250	7.9	7.5	94	10	0.95	1000	Sand	0.8	2	0.20	1	0.10	3
16	15.5	15.0	0.6	5	2250	7.9	7.5	94	2.5	0.95	700	Muddy sand	1.1	6	2.40	1	0.40	7
17	17.5	15.0	0.7	6	2250	8.0	7.7	100	9	0.11	1300	Muddy sand	1.4	10	1.10	31	3.44	95
18	17.2	15.0	1.0	8	2920	7.9	7.8	95	10	0.40	700	Sand	1.7	9	0.90	53	5.30	66

Table XIX. (continued)

Area No.	W.T. °C	S.T. °C	W. Vel. ft/sec	Av. depth in.	W at 18°C pH	S pH	O ₂ % Satn.	Area. m ²	I.L. factor	Soil comp.	Soil Type	Miles to Sp.G.	Total P.m. m ²	P.m. m ²	Total E.L. m ²	E.L. m ²	Total mm.	
19	16.2	14.0	1.2	10	3000	8.0	7.9	92	20	0.20	700	Sand	1.9	1	0.05	4	0.20	9
20	17.3	16.0	0.5	3	3000	8.2	7.7	94	10	1.00	400	Muddy sand	2.1	15	1.50	19	1.90	54
21	16.5	15.5	1.5	11	2850	8.2	7.8	94	12	0.50	1600	Sand	2.3	1	0.08	0	0.00	1
22	18.0	16.5	1.0	11	2850	8.1	7.8	96	7	0.04	550	Muddy sand	2.8	3	0.40	11	1.58	14
23	18.0	17.0	0.2	5	2850	8.1	7.6	96	2.2	0.05	0	Muddy sand	2.8	32	14.20	19	8.44	51
24	17.2	16.0	0.3	3	3120	8.1	7.6	99	4.5	0.60	0	Muddy sand	3.1	35	7.77	2	0.44	39
25	17.0	15.5	1.0	6	3120	8.1	7.9	99	6	0.02	400	Clay, med. sand	3.4	4	0.66	6	1.00	10
26	18.5	18.0	0.8	4	2800	8.0	8.4	90	8	0.50	500	Sand	3.5	0	0.00	0	0.00	0
27	16.0	15.5	0.3	1	3000	8.1	7.6	93	28	0.25	700	Mud	4.3	0	0.00	10	0.35	10
28	14.0	14.0	0.7	6	3300	8.0	7.6	90	16	0.27	700	Muddy sand	4.3	0	0.00	5	0.31	5
29	16.0	15.0	0.8	3	3300	8.3	7.8	88	16	0.57	400	Sand, clay	4.4	0	0.00	0	0.00	0
30	13.5	13.0	0.5	3	3560	8.2	7.9	95	3	0.16	600	Clay, sand, mud	3.7	0	0.00	6	2.00	6
31	14.2	14.0	1.5	12	3560	8.3	7.8	95	10	0.66	600	Sand	4.0	16	1.60	18	1.80	34
32	14.2	14.0	1.0	3	3560	8.3	7.8	95	5	0.44	400	Muddy sand	4.0	21	4.20	16	3.20	37
33	14.5	14.0	1.0	10	3400	8.4	7.6	99	5	1.00	400	Sand	4.7	11	2.20	3	0.60	14
34	14.5	14.0	1.0	8	3400	8.4	7.7	99	12	0.57	700	Sand	5.0	0	0.00	5	0.42	5
35	15.3	15.0	0.7	9	3400	8.4	7.9	99	5	0.63	800	Muddy sand	5.2	40	8.00	23	4.60	63
36	12.0	12.5	1.5	12	3420	8.1	7.6	96	20	0.88	900	Sand	4.5	1	0.05	5	0.25	6

Table XIX. (continued)

Area No.	W.T. °C	S.T. °C	W. Vel. ft/sec	Avg. depth in.	Av. $\wedge$ -cm ³ at 18°C	W pH	S pH	O ₂ % Satn.	Area m ²	I.L. factor	Soil Comp.	Soil Type	Miles to Sp.G.	Total P.m. m ²	P.m. per m ²	Total E.l. m ²	E.l. per m ²	Total amm.
37	13.0	13.0	0.7	6	3420	8.1	7.7	99	8	0.66	600	Muddy sand	5.4	12	1.50	14	1.75	26
38	13.0	13.0	0.8	6	3350	8.3	7.8	95	6	0.83	500	Muddy sand	5.7	2	0.33	2	0.33	4
39	14.0	13.5	0.6	9	3350	8.3	7.6	101	10	0.23	350	Muddy sand	5.9	14	1.40	13	1.30	27
40	13.5	12.5	1.0	9	3420	8.3	7.6	104	12	0.39	1000	Sand	5.4	0	0.00	2	0.17	2
41	11.8	11.0	1.0	6	3500	8.2	7.8	100	9	0.44	1400	Sand	5.4	0	0.00	0	0.00	0
42	13.0	13.0	1.5	8	3200	8.4	7.8	98	45	1.00	700	Sand	6.4	3	0.07	8	0.18	11
43	13.0	13.0	0.7	2	3200	8.4	7.5	98	3	1.00	0	Muddy sand	6.4	6	2.00	2	0.67	8
44	13.0	13.0	0.1	6	3200	8.3	7.8	98	2	0.43	600	Muddy sand	7.2	9	4.50	9	4.50	19
45	15.0	14.5	1.0	12	2980	8.2	7.8	88	12	1.00	500	Sand	6.7	33	2.75	48	4.00	82
46	15.0	14.5	0.3	10	2980	8.2	7.5	88	9	0.90	1000	Sand	6.9	5	0.56	10	1.11	15
47	15.0	14.5	0.3	6	3060	8.2	7.7	88	9	1.00	450	Muddy sand	7.6	82	9.10	52	5.77	134

Table XX. Correlation coefficients for relationships between population densities of P. marinus and E. (L.) lamottei, bottom compactness and water velocity.

Correlation investigated	"r"	Degrees of freedom	Necessary "r" for significance at level	
			1%	5%
<u>P. marinus</u> x <u>E. (L.) lamottei</u>	+0.77	46	+0.372	+0.288
Compactness x velocity	+0.24	"	"	"
<u>P. marinus</u> x compactness	-0.44	"	"	"
<u>E. (L.) lamottei</u> x compactness	-0.30	"	"	"
<u>P. marinus</u> x velocity	-0.44	"	"	"
<u>E. (L.) lamottei</u> x velocity	-0.41	"	"	"

Table XXI. Venison Creek at Concession No. 8 ammocoete bed bottom composition record.

Date 1958	S i e v e s															
	#4		#6		#8		#18		#30		#60		#200		B	
	0	I	0	I	0	I	0	I	0	I	0	I	0	I	0	I
17 Jul.	..	..	..	..	..	..	..	1	..	3	..	75	..	..	..	21
24 "	2	..	..	1	..	1	2	2	..	40	..	40	..	..	..	12
31 "	1	..	..	..	..	..	3	..	2	3	..	60	..	30	..	1
7 Aug.	5	..	1	..	1	..	3	2	2	5	..	50	..	30	..	1
15 "	1	..	1	..	1	..	1	..	2	..	..	60	..	30	..	4
21 "	10	..	2	..	2	..	5	..	5	..	5	25	..	42	..	4
28 "	15	..	1	..	1	..	5	..	5	..	..	10	..	56	..	5
4 Sep.	10	..	2	..	2	..	5	2	3	2	..	33	..	33	..	4
11 "	10	..	2	..	2	..	5	..	5	..	5	35	..	35	..	1
19 "	10	..	1	..	1	..	2	..	3	..	1	40	..	40	..	2
2 Oct.	15	..	2	..	2	..	5	..	5	..	..	35	..	35	..	1
9 "	10	..	1	..	1	..	5	..	5	1	5	30	..	40	..	2
16 "	25	..	5	..	3	..	5	..	2	2	2	25	..	39	..	2
23 "	20	..	3	..	2	..	10	..	5	2	..	40	..	26	..	2
31 "	25	..	5	..	3	..	5	..	3	3	2	25	..	30	..	1
6 Nov.	30	..	5	..	3	..	10	1	5	..	..	23	..	20	..	1
20 "	10	..	1	..	1	..	3	3	..	10	..	50	..	20	..	2

0 = Organic matter.
I = Inorganic matter.

Table XXII. Venison Creek at Concession No. 8 ammocoete bed, bottom compactness record.

Date 1958	Compactness in g/ ²			Total P.m.*	Total E.(L.)l.**
	Max.	Min.	Mean		
17 Jul.	2000	1000	1700	48	46
24 "	1000	200	800	89	21
31 "	1600	800	1200	74	19
7 Aug.	+2000	1400	+2000	92	21
15 "	2000	200	+2000	101	36
21 "	+2000	600	+2000	95	18
28 "	+2000	1600	2000	161	28
4 Sep.	+2000	900	1800	80	33
11 "	+2000	800	+2000	125	114
19 "	+2000	1400	+2000	99	79
2 Oct.	+2000	800	+2000	60	71
16 "	+2000	800	+2000	28	59
23 "	+2000	1400	+2000	24	55
31 "	+2000	800	+2000	52	58
6 Nov.	+2000	1800	+2000	63	46
20 "	+2000	800	+2000	54	71

*P.m. = Petromyzon marinus.

**E.(L.)l. = Entosphenus (Lampetra) lamottei.

Table XXIII. Lamprey movement through Stony Creek weirs.

Lamprey	Direction of movement	May*	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.*	Total	Total
<u>P. marinus</u> (adult)	Up	19	6	0	0	0	0	0	0	0	25	48
	Down	16	7	0	0	0	0	0	0	0	23	
<u>P. marinus</u> (newly transformed)	Up	0	0	0	0	0	0	0	0	0	0	65
	Down	0	0	0	0	1	0	23	25	16	65	
<u>P. marinus</u> (ammocoete)	Up	0	0	0	0	0	0	0	0	0	0	232
	Down	83	52	32	12	16	10	14	6	7	232	
<u>E. (L.) lamottei</u> (adult)	Up	36	0	0	0	0	0	0	0	0	36	163
	Down	127	0	0	0	0	0	0	0	0	127	

*Incomplete months.

Table XXIV. Monthly catch of P. marinus ammocoetes in Stony Creek weir compared with monthly mean flow (North Cr.) and monthly mean temperature (1958).

Month	Ammocoetes caught	Mean flow cfs	Mean Temperature °F
Jun.	53	10	61
Jul.	32	9	62
Aug.	12	6	60
Sep.	16	7	56
Oct.	10	8	46
Nov.	14	10	39
Dec.	6	10	34

Table XXV. Monthly catches of ammocoetes at Venison Creek Concession #8 re-shocking station, with concurrent mean flow, source of run-off, and temperature data.

Year	Month	No. <u>P. marinus</u>	No. <u>E. (L.) lamottei</u>	Mean flow (cfs)	Mean temp. (°F)	Source of run-off (in)
1957	Jul.	165	70	14	58	3.3
	Aug.	290	83	15	57	5.5
	Sep.	301	227	19	54	5.2
	Oct.	35	36	15	48	2.4
	Nov.	26	74	29	44	3.4
	Dec.	11	23	41	41	4.7
1958	Jan.	17	40	17	37	0.7
	Feb.	10	16	15	34	2.7
	Mar.	N.A.	N.A.	30	41	0.8
	Apr.	94	101	22	48	2.6
	May	184	268	10	51	1.9
	Jun.	390	278	10	54	4.2
	Jul.	242	104	9	59	2.3
	Aug.	472	136	6	58	2.1
	Sep.	323	275	7	55	3.4
	Oct.	109	178	8	50	1.1
	Nov.	119	122	10	44	1.9
	Dec.	11	34	10	35	1.3
1959	Jan.	8	10	18	35	N.A.

N. A. = Data not available.

Table XXVI. Simple and multiple correlation coefficients for comparisons of the number of ammocoetes caught at the re-shocking area, Concession #8, Venison Creek, with temperature, flow, and source of run-off.

	Water temp. (°F.)	Flow (cfs)	Source of run-off	Temp. + flow	Temp. + run-off
No. of <u>P. marinus</u> caught	+0.82* d.f. = 17	-0.50** d.f. = 17	+0.33 d.f. = 16	+0.72* d.f. = 16	+0.81* d.f. = 15
No. <u>E. (L.) lamottei</u> caught	+0.60* d.f. = 17	-0.45 d.f. = 17	+0.15 d.f. = 16	+0.65* d.f. = 16	+0.52** d.f. = 15

*Significant at 1% level.

**Significant at 5% level.

d.f. = degrees of freedom.

Table XXVII. Age of most abundant ammocoetes and minimum size of ammocoetes found at major sampling stations on Venison Creek.

Con. of station	Miles below lowest <u>P. marinus</u> spawning	Minimum size found (in mm)		Most abundant year-class	
		<u>E. (L.) l.*</u>	<u>P.m.**</u>	<u>E. (L.) l.*</u>	<u>P.m.**</u>
12	0.0	16	9	0+	0+
12	0.5	17	16	0+	0+
8	3.5	32	10	1+	1+
8	4.5	28	26	2+	2+
5	7.2	37	24	3+	3+

*E. (L.) l. = E. (L.) lamottei.

**P.m. = P. marinus.

Table XXVIII. Periods of activity for each hour of darkness with approximate number of contacts. $50^{\circ}\text{F} \pm 1^{\circ}\text{F}$. Light 12 hours on, 12 hours off.

1800-1900		1900-2000		2000-2100		2100-2200	
Per.	Cont.	Per.	Cont.	Per.	Cont.	Per.	Cont.
...	...	4	23+	2	7+	2	2
2200-2300		2300-2400		0000-0100		0100-0200	
Per.	Cont.	Per.	Cont.	Per.	Cont.	Per.	Cont.
1	1	2	2+	2	3	3	5
0200-0300		0300-0400		0400-0500		0500-0600	
Per.	Cont.	Per.	Cont.	Per.	Cont.	Per.	Cont.
...	...	...	...	...	...	...	...

Table XXIX. Periods of activity for each hour of darkness with approximate number of contacts. $50 \pm 1^{\circ}\text{F}$. Light 18 hours on, 6 hours off.

1800-1900		1900-2000		2000-2100		2100-2200	
Per.	Cont.	Per.	Cont.	Per.	Cont.	Per.	Cont.
3	8+	8	20+	7	18+	2	2
2200-2300		2300-2400					
Per.	Cont.	Per.	Cont.				
5	6+	...	...				

Table XXX. Periods of activity for each hour of darkness with approximate number of contacts. $60 \pm 1^{\circ}\text{F}$. Light 18 hours on, 6 hours off.

1800-1900		1900-2000		2000-2100		2100-2200	
Per.	Cont.	Per.	Cont.	Per.	Cont.	Per.	Cont.
3	3+	8+	16	6	7	7	8
2200-2300		2300-2400					
Per.	Cont.	Per.	Cont.				
4	11+	2	24+				

Table XXXI. Summary of results from activity experiments.

Expt.	Temp. $^{\circ}\text{F}$	Duration	No. Periods		Periods per day	No. Contacts		Contacts per day
			Dark	Light		Dark	Light	
1	50	21 days	14	2	0.76	41+	2	2.10+
2	50	28 days	25	0	0.89	54+	0	1.93+
3	60	22 days	28	2	1.36	69+	4+	3.32+

Table XXXII. Swimming speeds of ammocoetes in the laboratory.

Length (mm)	Mean spontaneous speed ft/sec.	Mean maximum speed ft/sec.	Maximum recorded speed ft/sec.
<u>P. marinus</u> at 4-7°C			
140	0.34	0.87	1.20
122	0.31	0.56	0.75
112	0.32	0.63	0.75
84	0.30	0.64	0.72
80	0.20	0.45	0.50
75	0.28	0.50	0.56
69	0.25	0.50	0.57
65	0.20	0.48	0.57
57	0.20	0.52	0.57
31	0.13	0.32	0.45
<u>E. (L.) lamottei</u> at 5-7°C			
128	0.21	0.56	0.67
119	0.15	0.24	0.29
86	0.22	0.36	0.50
54	0.16	0.37	0.44
<u>E. (L.) lamottei</u> at 10°C			
176	0.57	1.24	1.55
108	0.27	0.43	0.50

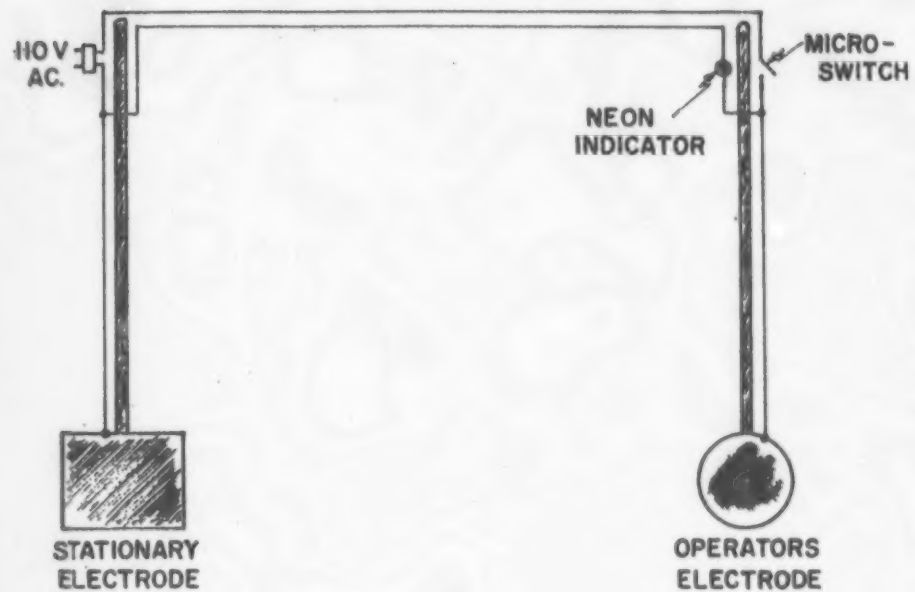


Fig. 1. Shocking electrode circuit.

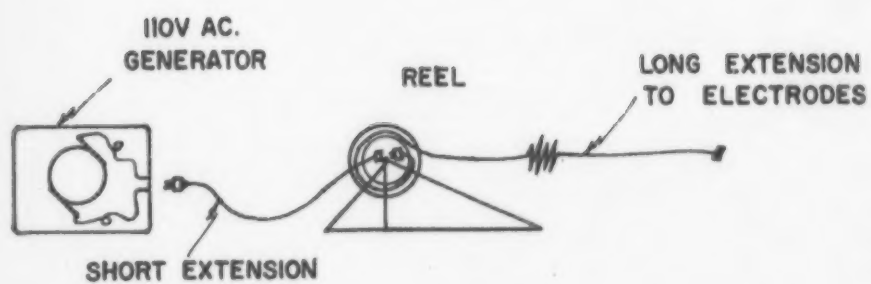


Fig. 2. Extension cord set up (diagramatic).

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Fig. 3. Shocking equipment.

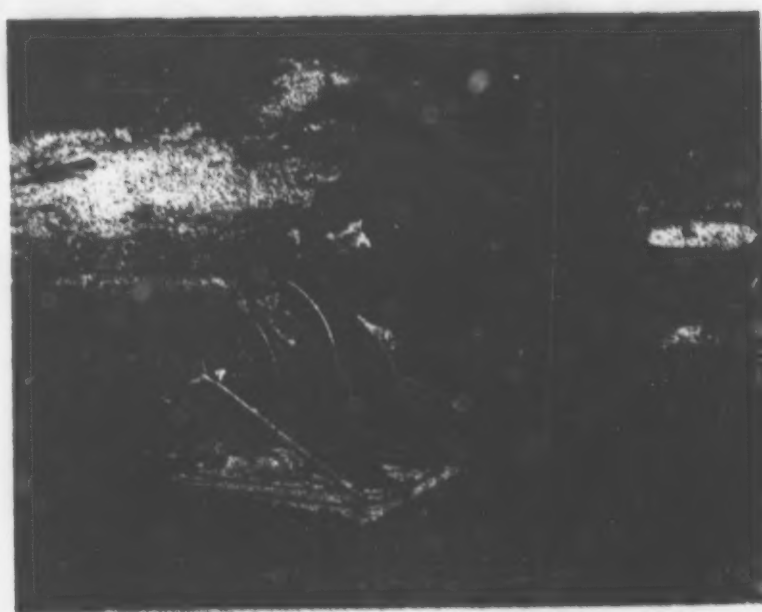


Fig. 4. Cable reel in operation.

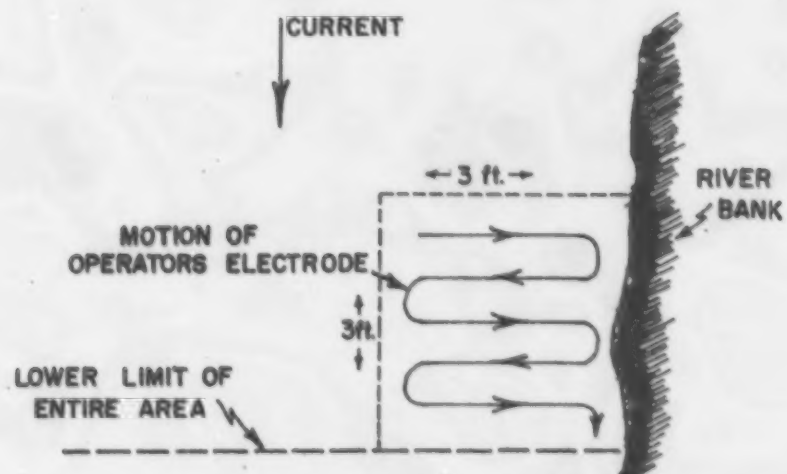


Fig. 5. Shocking technique (detail).

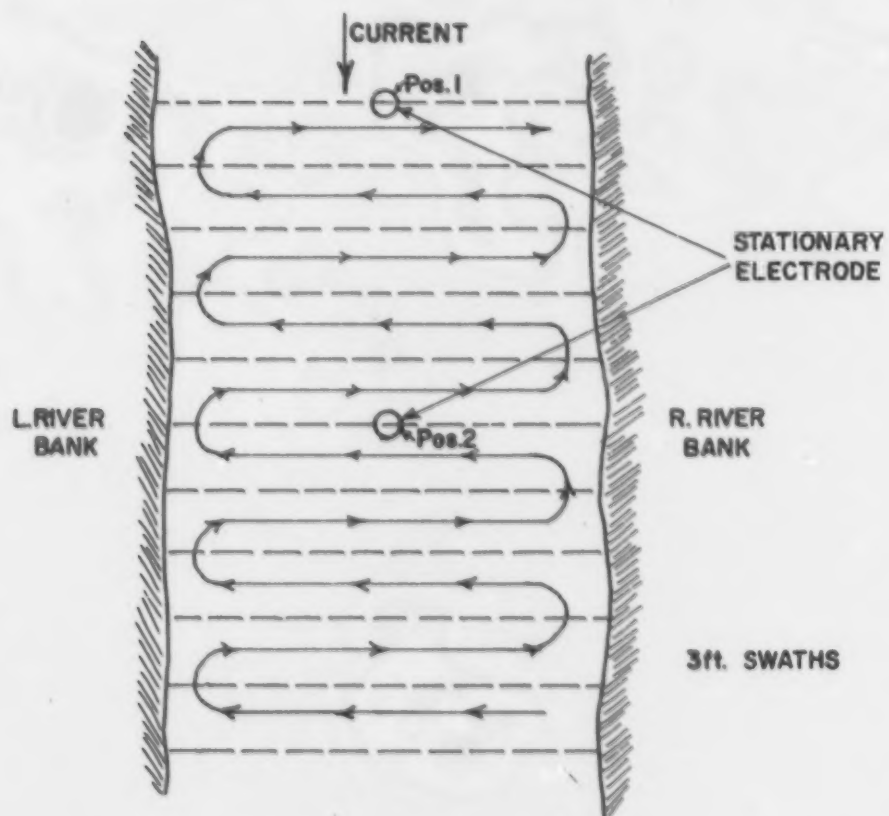


Fig. 6. Shocking technique (general plan).



Fig. 7. Shocking in Venison Creek.



Fig. 8. Double V-type trap weirs used to trap migrating ammocoetes, in operation in Stony Creek.

FISHERIES RESEARCH BOARD OF CANADA
AMMOCOETE STUDIES

AMMOCOETE SAMPLE RECORD SHEET 1

DATE: DAY: TIME:

Cloud Cover..... Wind Direction..... Force
Air Temperature.....°F. Max. - Min..... °F. for 24 H.
Stream..... Map Ref.
Area Cleared..... Rainfall..... in.
Water Temperature.....°F. Substrate Temperature.....°F.
Water Turbidity..... Water Velocity..... Ft/Sec.
Water Depth..... Water Conductivity..... Ohms/CM³.
Water pH..... Water O₂.....p.p.m. Water CO₂.....p.p.m.
Substrate Compactness..... g.
Substrate Particle Size.....
Substrate General Nature.....
Substrate Stratification.....
Total P. marinus Total E. lamottei
Total Ichthyomyzon spp.

Diagram showing area sampled (indicate direction of current, any concentrations of ammocoetes, etc.) 1-

REMARKS:-

(Initials)

Fig. 9. Form used in recording data from stream sampling stations.



Fig. 10. Stony Creek trap weirs iced over in January 1959.

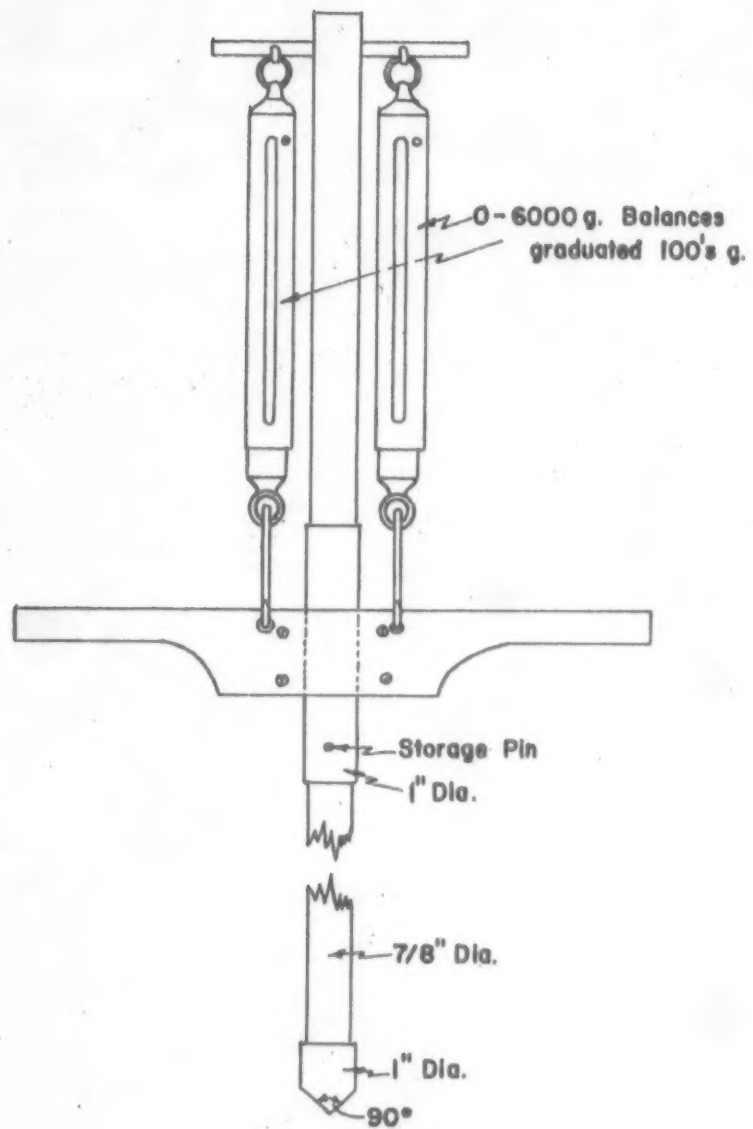


Fig. 11. Penetrometer showing construction details.

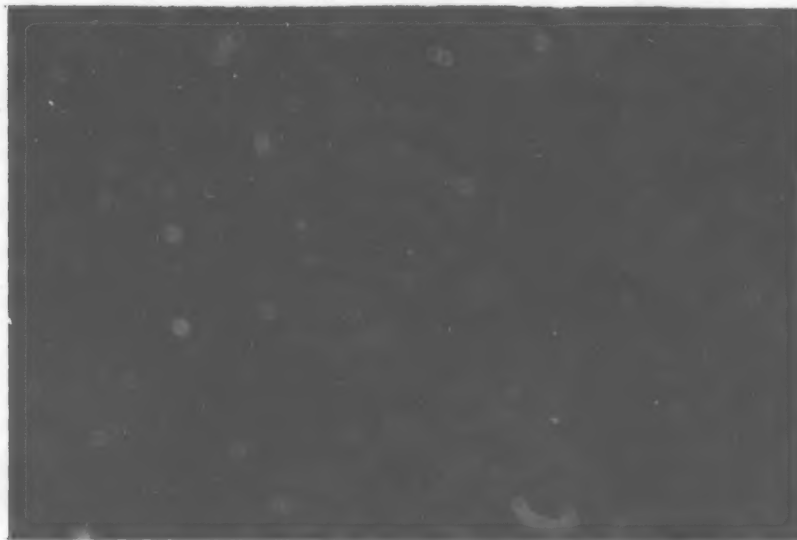


Fig. 12. Artificial stream in controlled illumination cabinet.



Fig. 13. Activity detector in place on artificial stream.

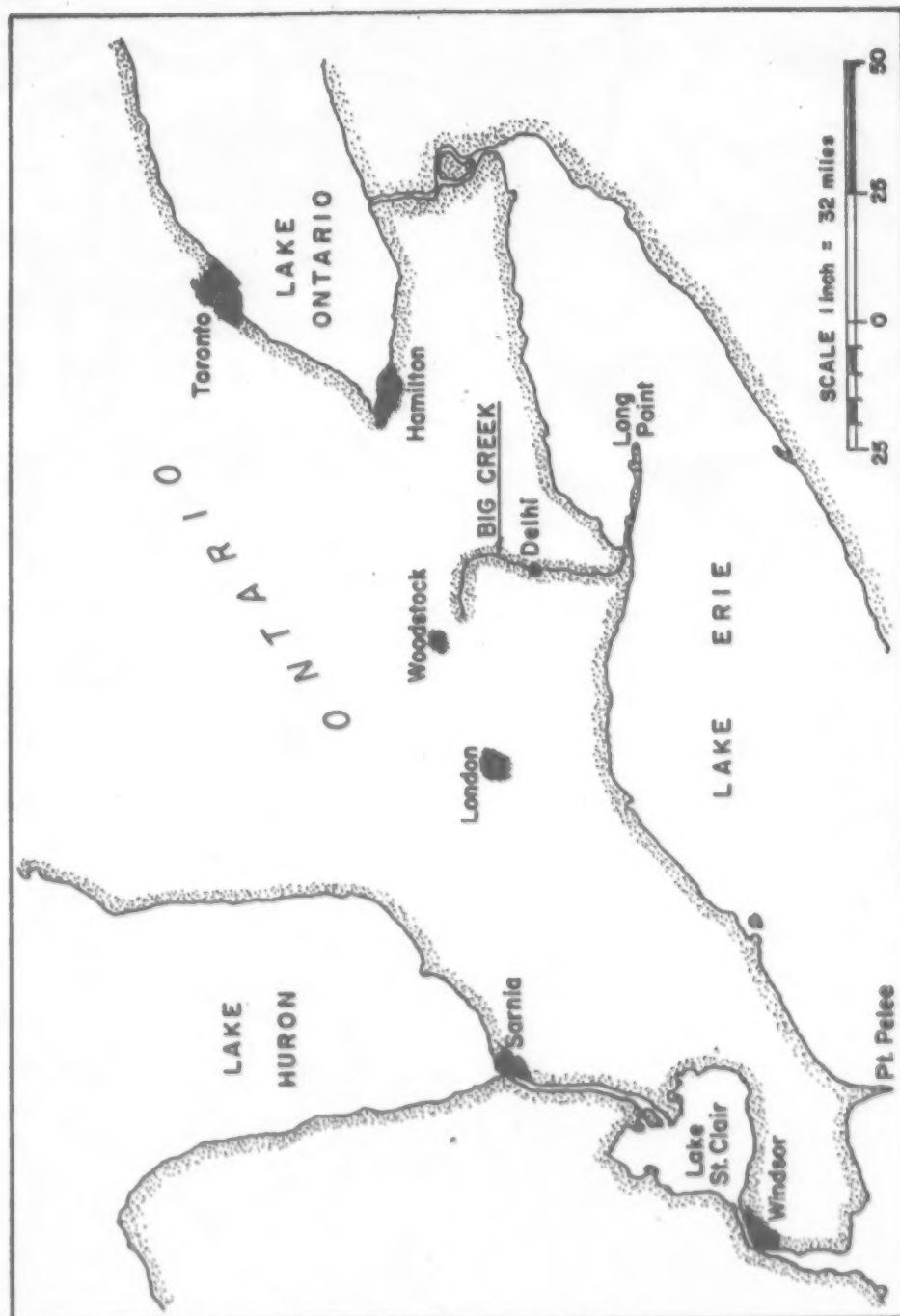


Fig. 14. Map of Southern Ontario showing the location of Big Creek watershed.



Fig. 15. Big Creek watershed.



Fig. 16. Big Creek in the west part of Burford Township flowing in dug channel through flat terrain.



Fig. 17. Big Creek flowing through the deltaic plains of Burford Township. It is slow and muddy.

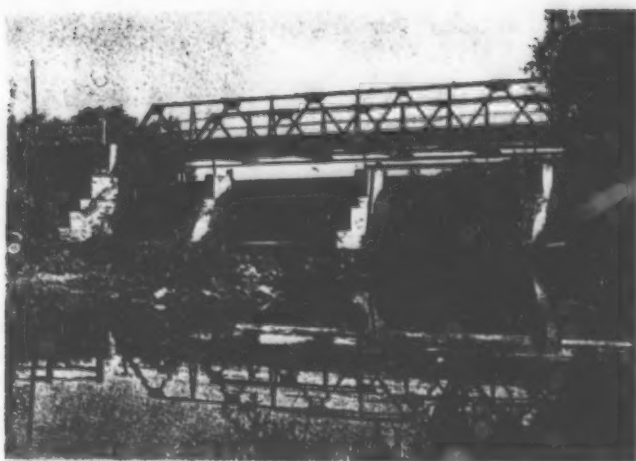


Fig. 18. Teeterville Dam, an effective barrier to fish and lamprey migration in Big Creek.



Fig. 19. Teeterville Lake, Big Creek.

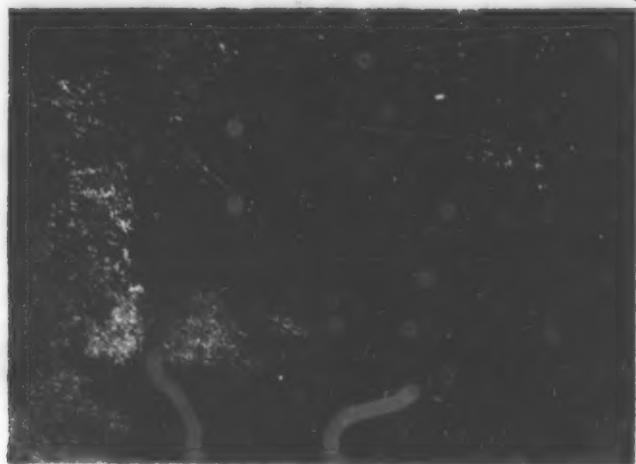


Fig. 20. Big Creek between Delhi and Teeterville showing typical sand bottom.



Fig. 21. Delhi Dam on Big Creek, a barrier to the upstream migration of fish and lampreys.



Fig. 22. Big Creek two miles below Delhi, showing typical lamprey spawning site.



Fig. 23. Big Creek at Lyndoch, where the bottom is typically of sand.



Fig. 24. Big Creek at Concession #5, S. Walsingham Twp. In these lower reaches the course is meandering and the bottom of mud.



Fig. 25. Leman's Dam on North Creek.

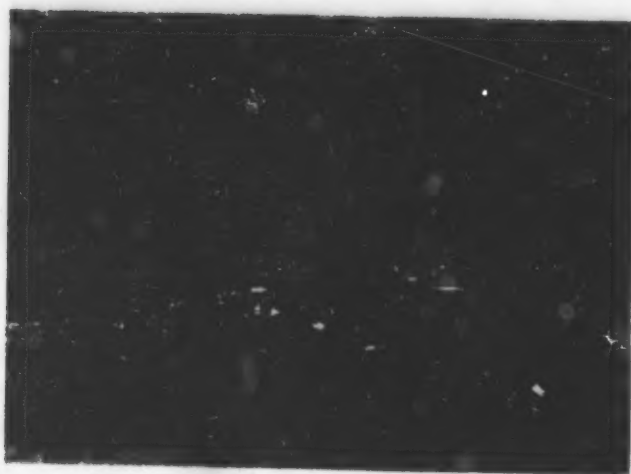


Fig. 26. Stony Creek showing typical lamprey spawning location in rapids.



Fig. 27. Cranberry Creek, where the chute is a barrier to upstream migration.



Fig. 28. Venison Creek Dam, which is a barrier to upstream migration of fish and lampreys.



Fig. 29. Typical silted ammocoete beds in Venison Creek.



Fig. 30. Typical lower course of Venison Creek with sand to mud bottom.

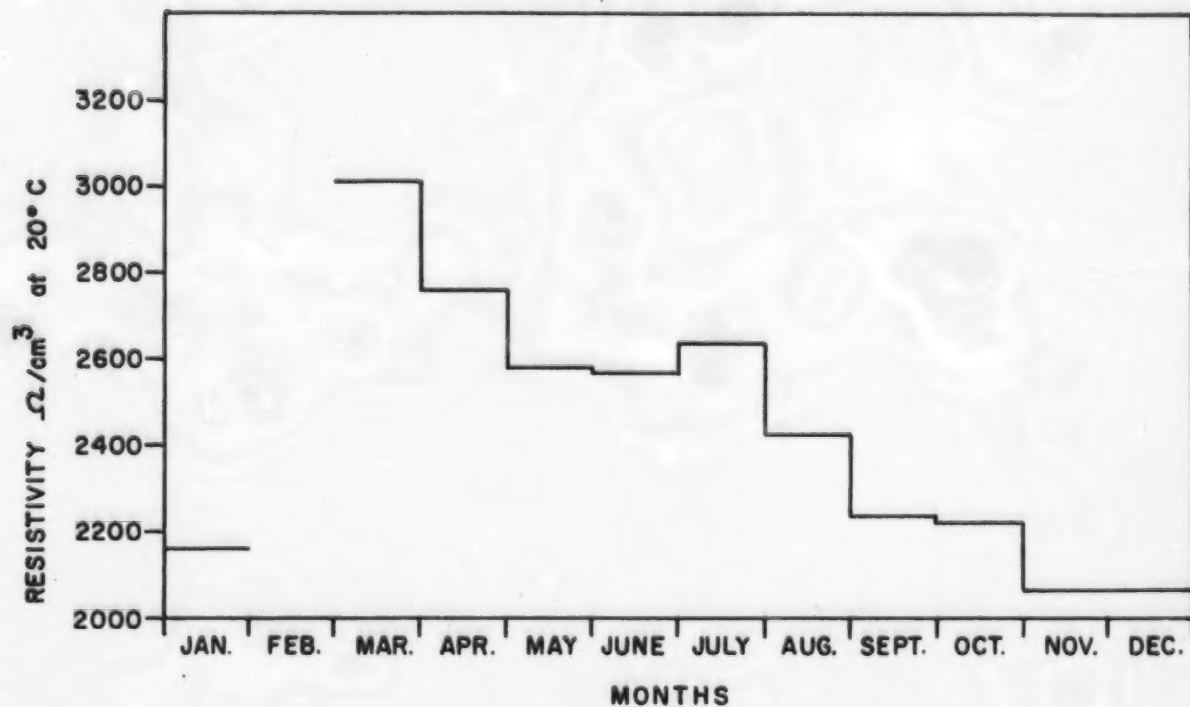


Fig. 31. Mean monthly resistivities in Stony Creek, 1957-1958.

Mean Water Temperature in Stony Cr. °F = $8.16 + 0.794$ (Mean Air Temperature Delhi °F)
 Mean Water Temperature in Venison Cr. °F = $25.51 + 0.479$ (Mean Air Temperature Delhi °F)
 (Above equations may only be used where resulting water temperature is above 32°F)

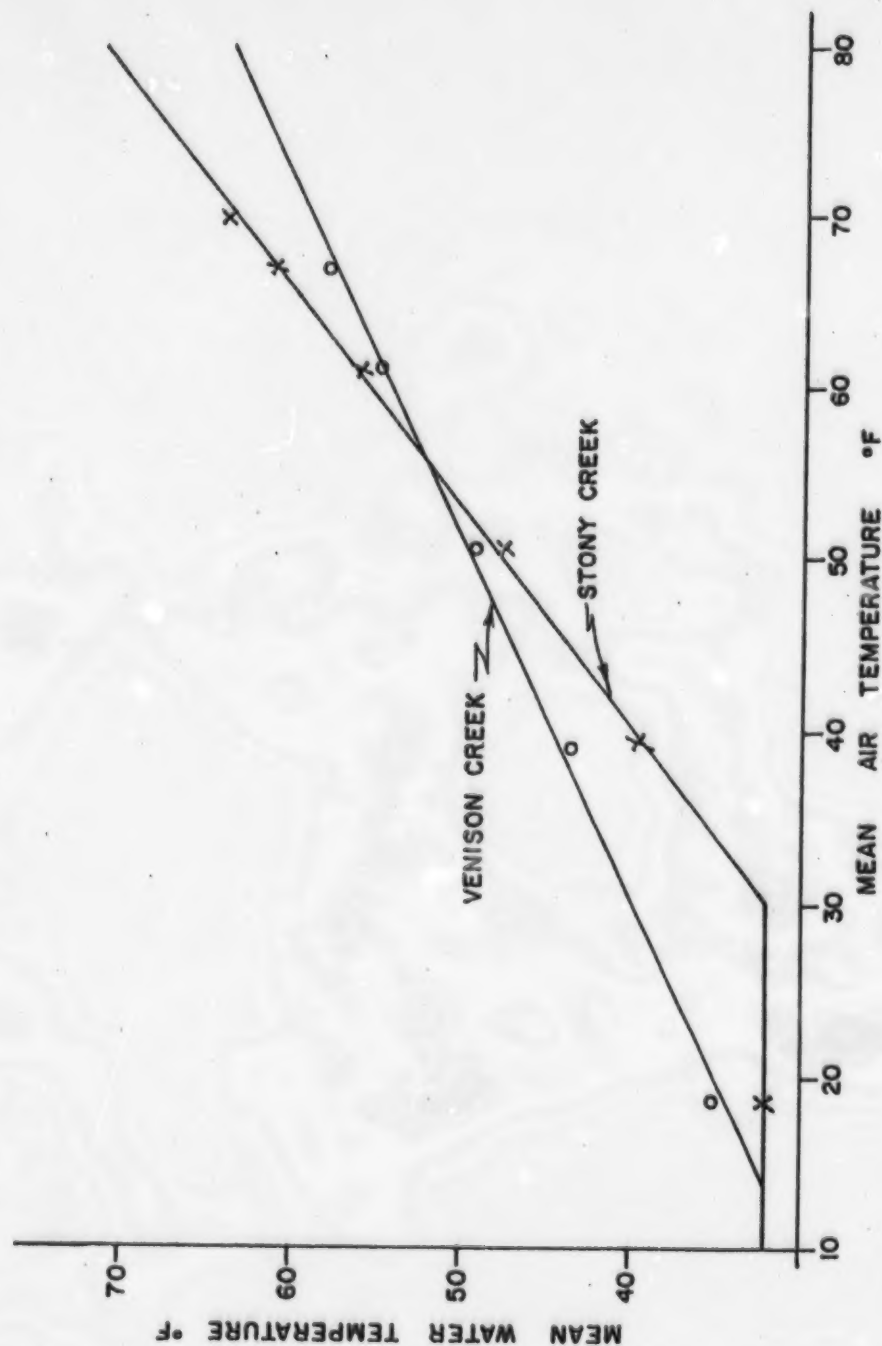


Fig. 32. Relationship between monthly mean air temperature at Delhi and monthly mean water temperatures in Venison and Stony Creeks.

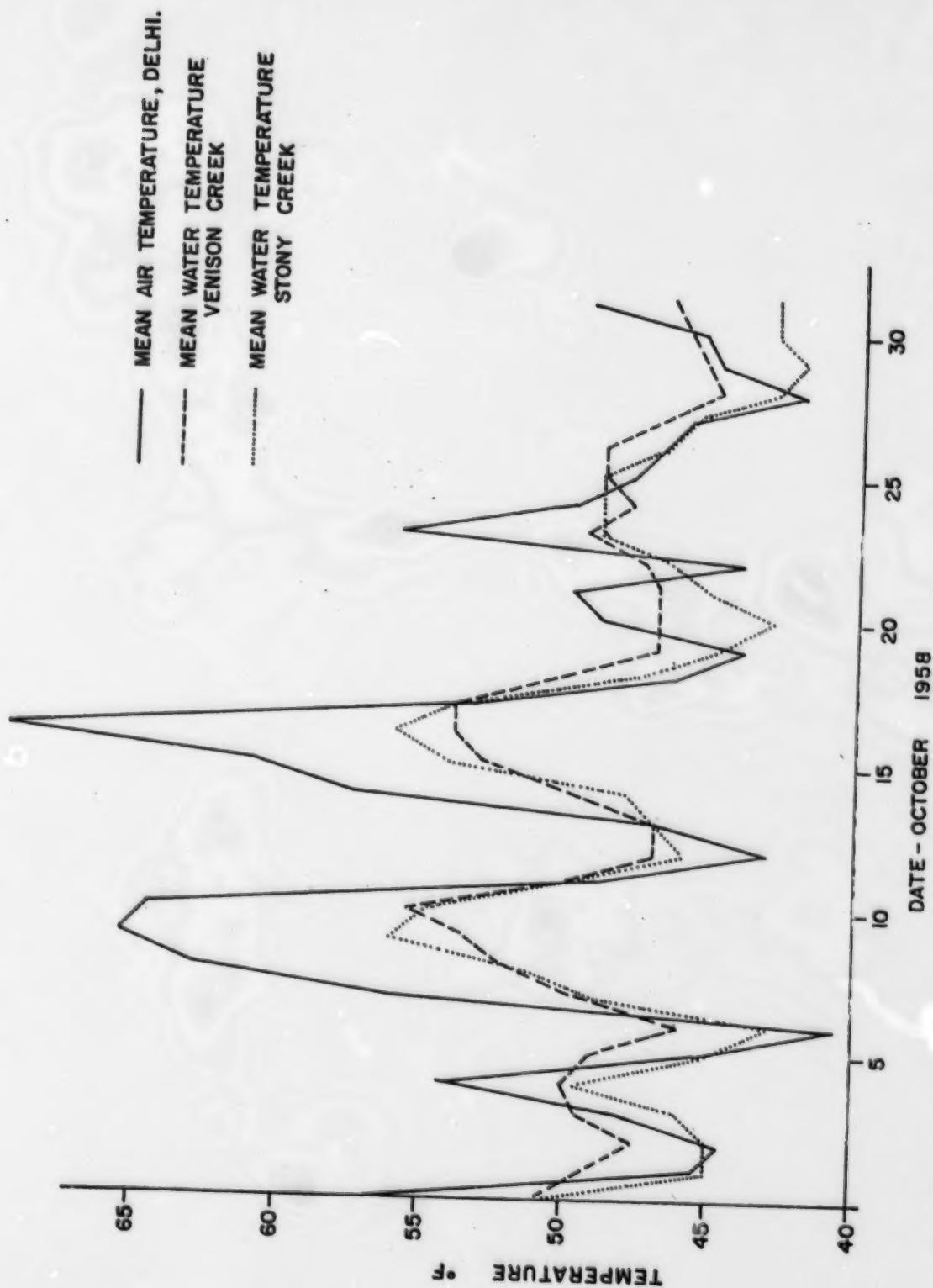


Fig. 33. Daily mean air temperature at Delhi and daily mean water temperatures in Stony and Venison Creeks during October 1958.

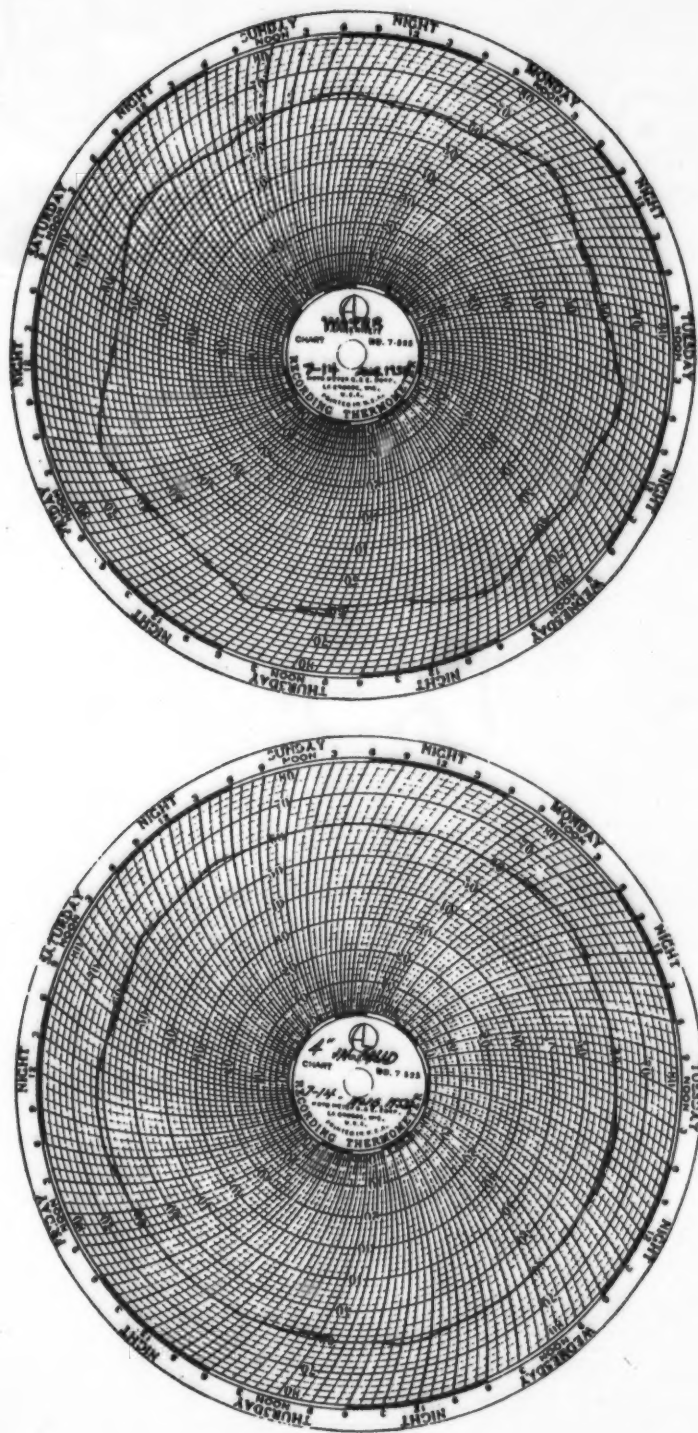


Fig. 34. Thermorecorder records from water (upper) and in the substratum (lower) in Venison Creek, August 7-14, 1958.

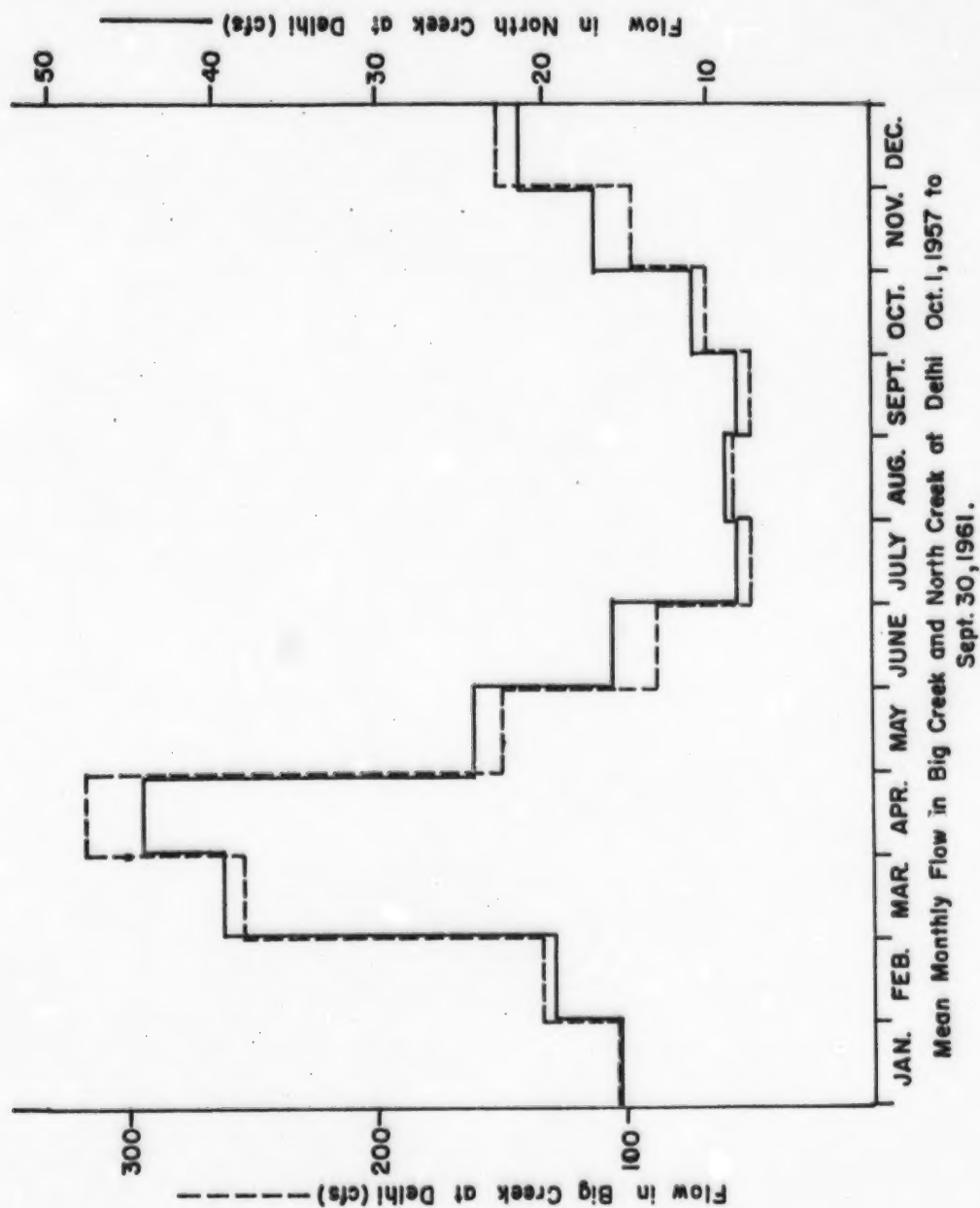


Fig. 35. Annual flow cycle in Big Creek and North Creek (North Branch) at Delhi, from data averaged from 1957-1961.

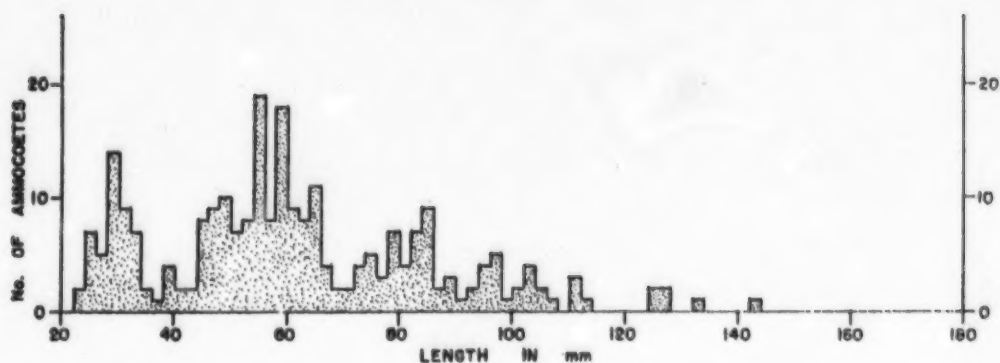


Fig. 36. Length-frequency diagram for 254 *P. marinus* caught at Concession #12, Venison Creek, January 17, 1961.

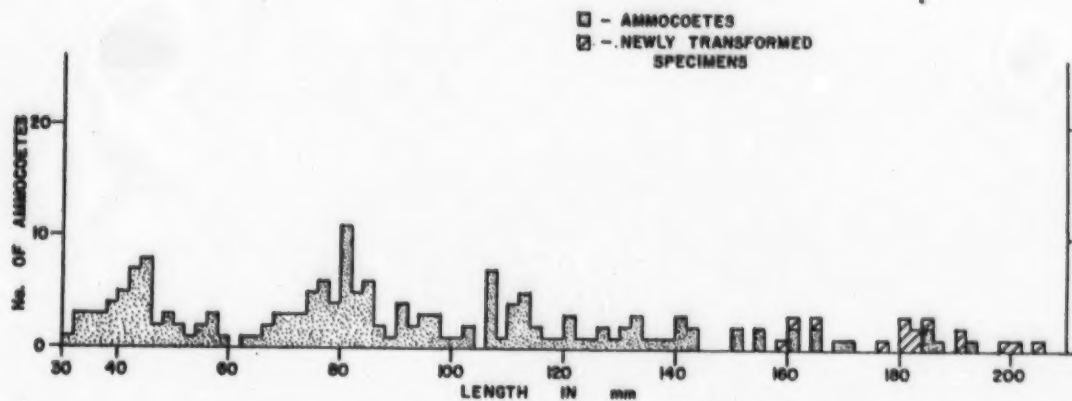


Fig. 37. Length-frequency diagram for 189 *E. (L.) lamottel* caught at Concession #12, Venison Creek, May 5, 1961.

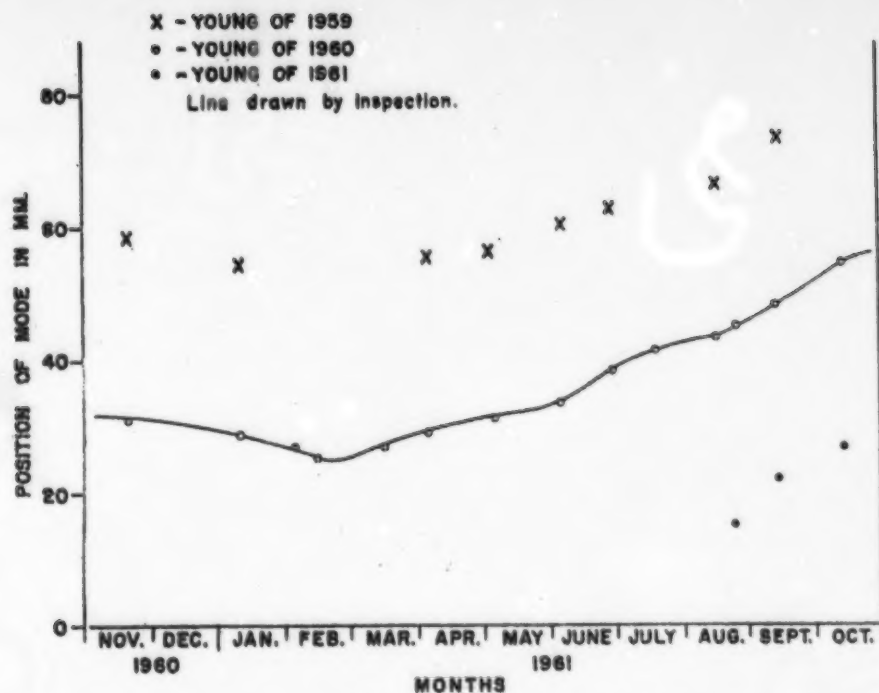


Fig. 38. Growth of P. marinus ammocoetes in Venison Creek during the year 1960-1961.

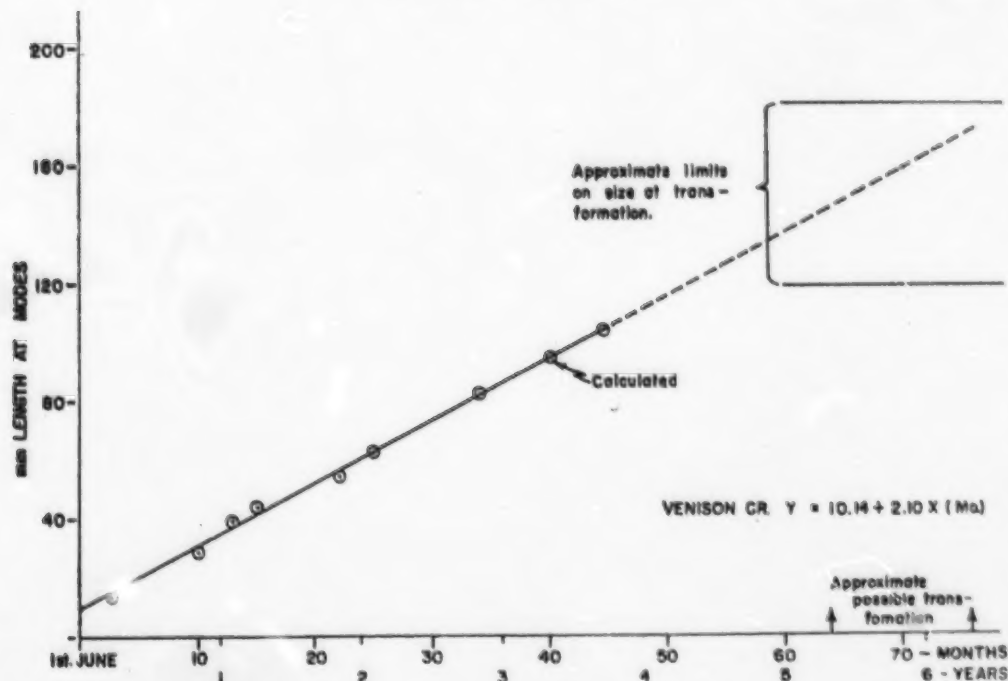


Fig. 39. Total growth of P. marinus ammocoetes in Venison Creek.

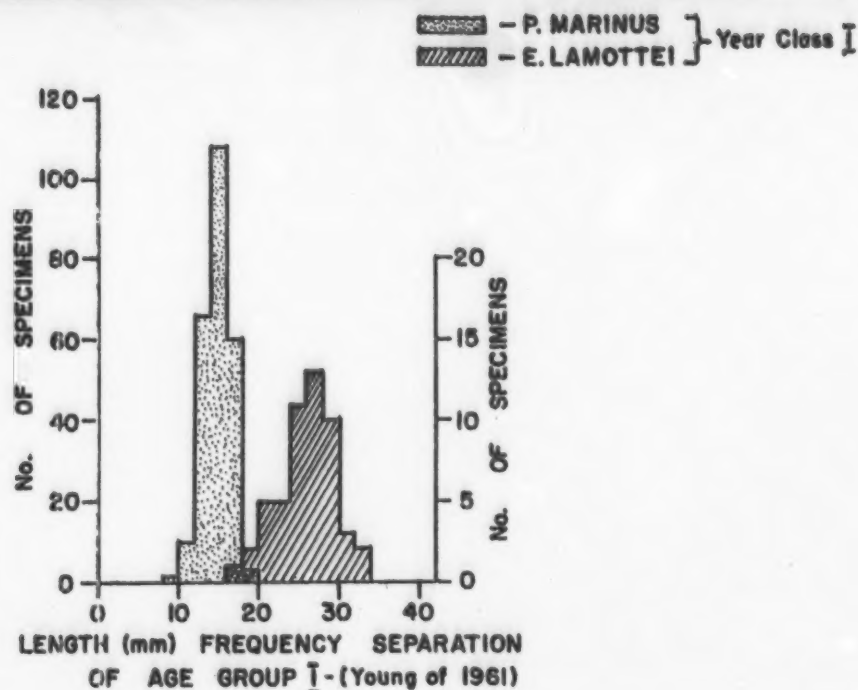


Fig. 40. Length-frequency diagrams of young-of-the-year E. (L.) lamottei and P. marinus caught August 24, 1961, at Concession #12, Venison Creek.

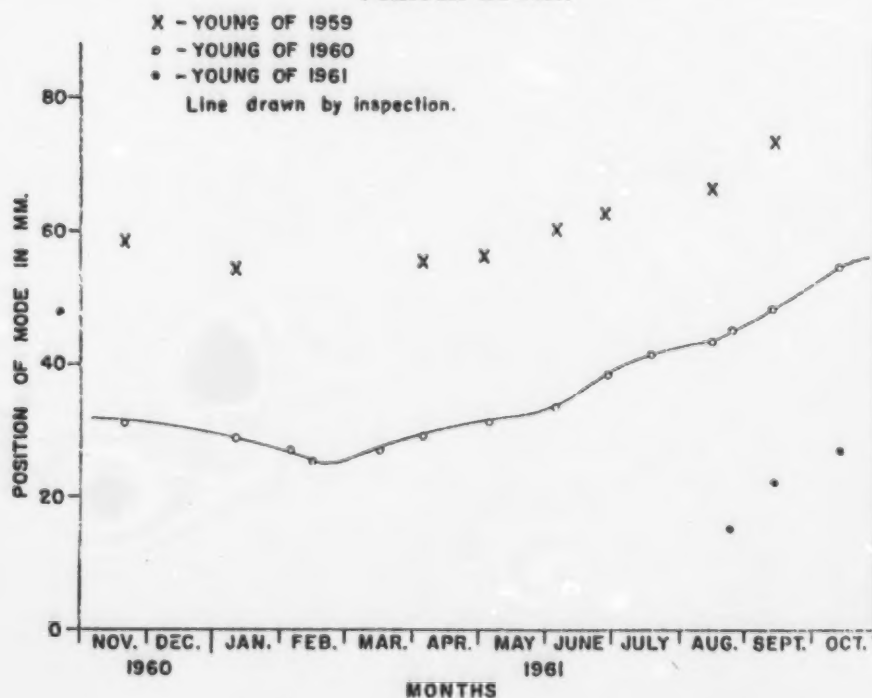


Fig. 41. Growth of E. (L.) lamottei ammocoetes in Venison Creek during the year 1960-1961.

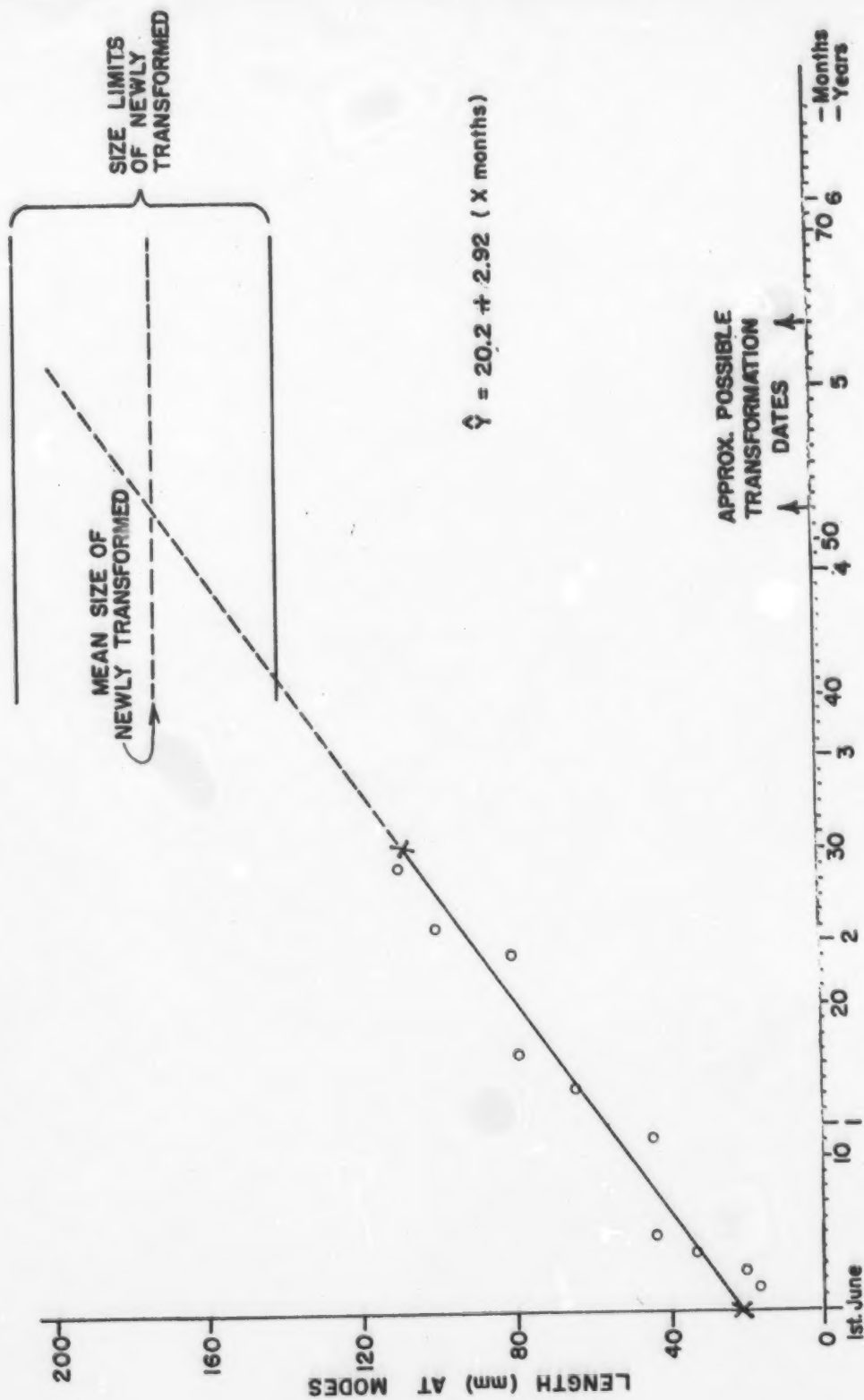


Fig. 42. Total growth of E. (L.) lamottei ammocoetes in Venison Creek.

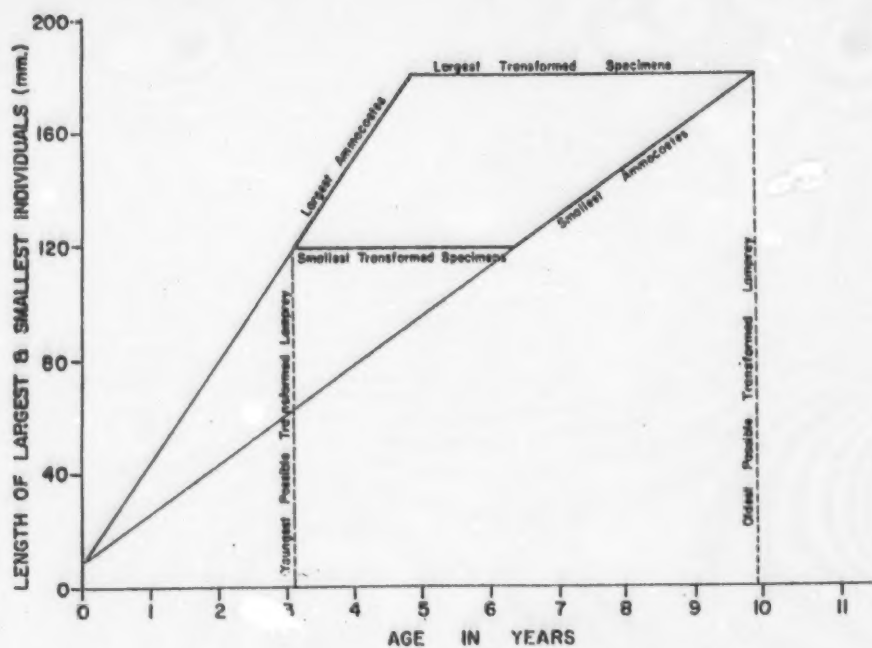


Fig. 43. Diagram showing the possible limits on the length of the larval period in *P. marinus* in Venison Creek.

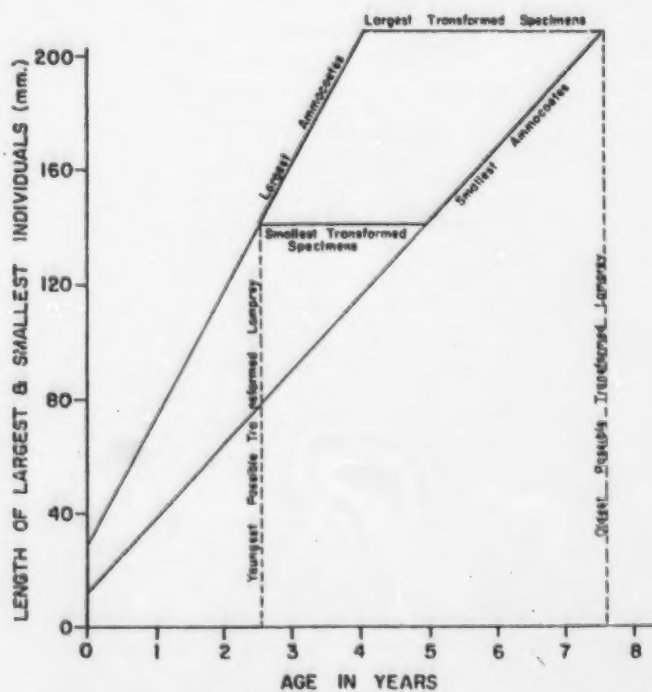


Fig. 44. Diagram showing the possible limits on the length of the larval period in *E. (L.) lamottei* in Venison Creek.

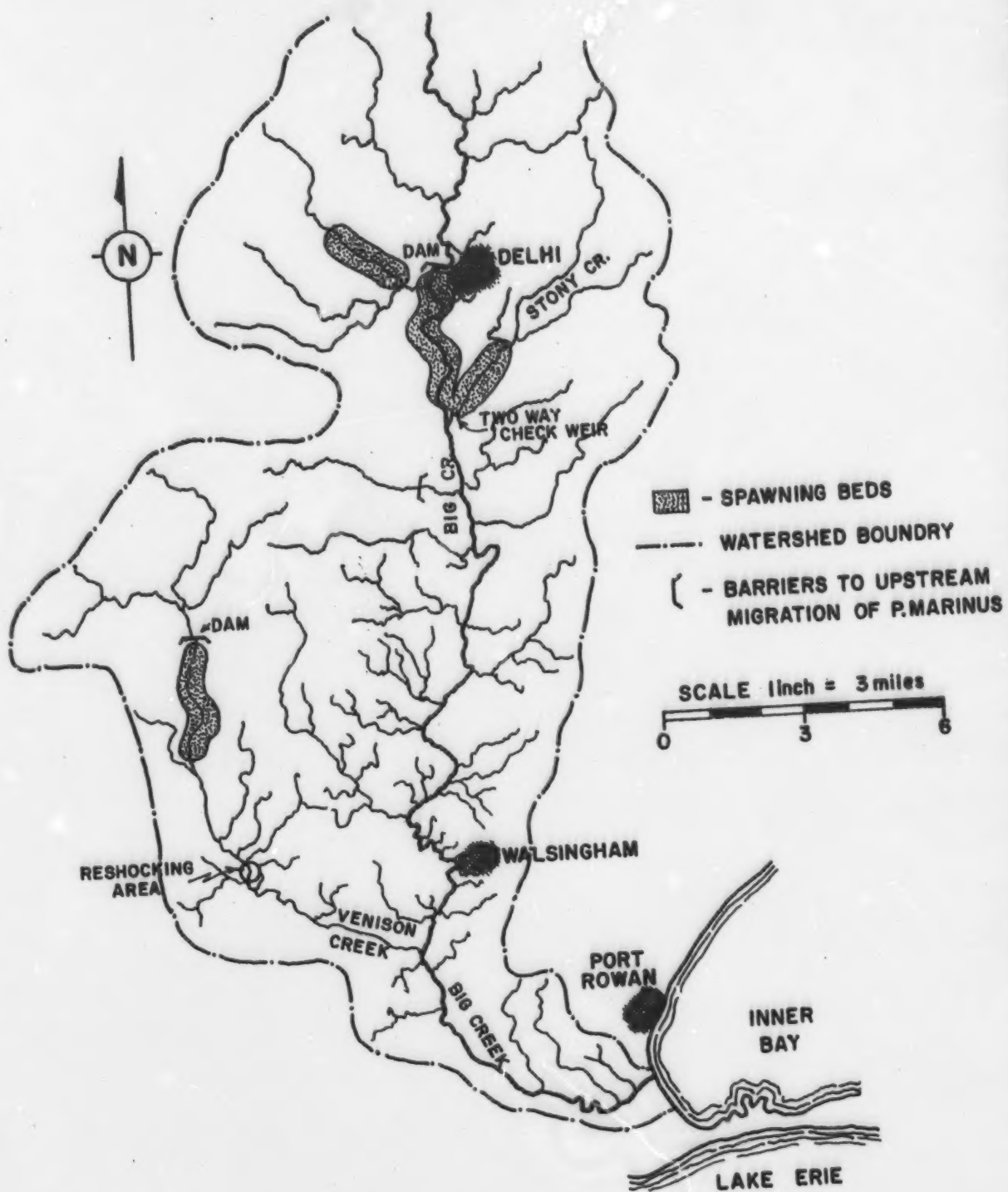


Fig. 45. Spawning sites of *P. marinus* in Big Creek.

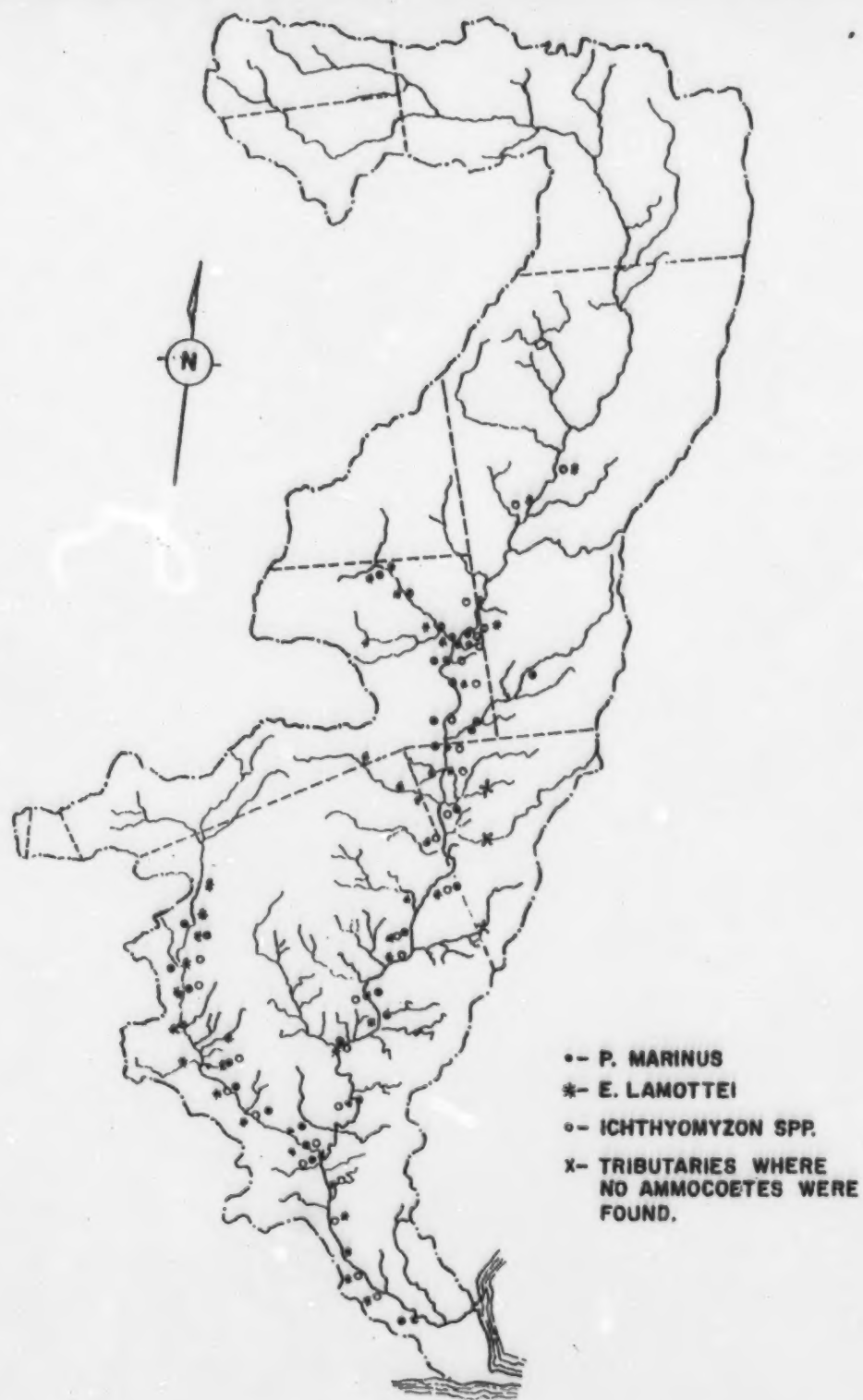


Fig. 46. Distribution of ammocoetes of *P. marinus*, *E. lamottei* and *Ichthyomyzon* spp. in Big Creek below Teeterville.

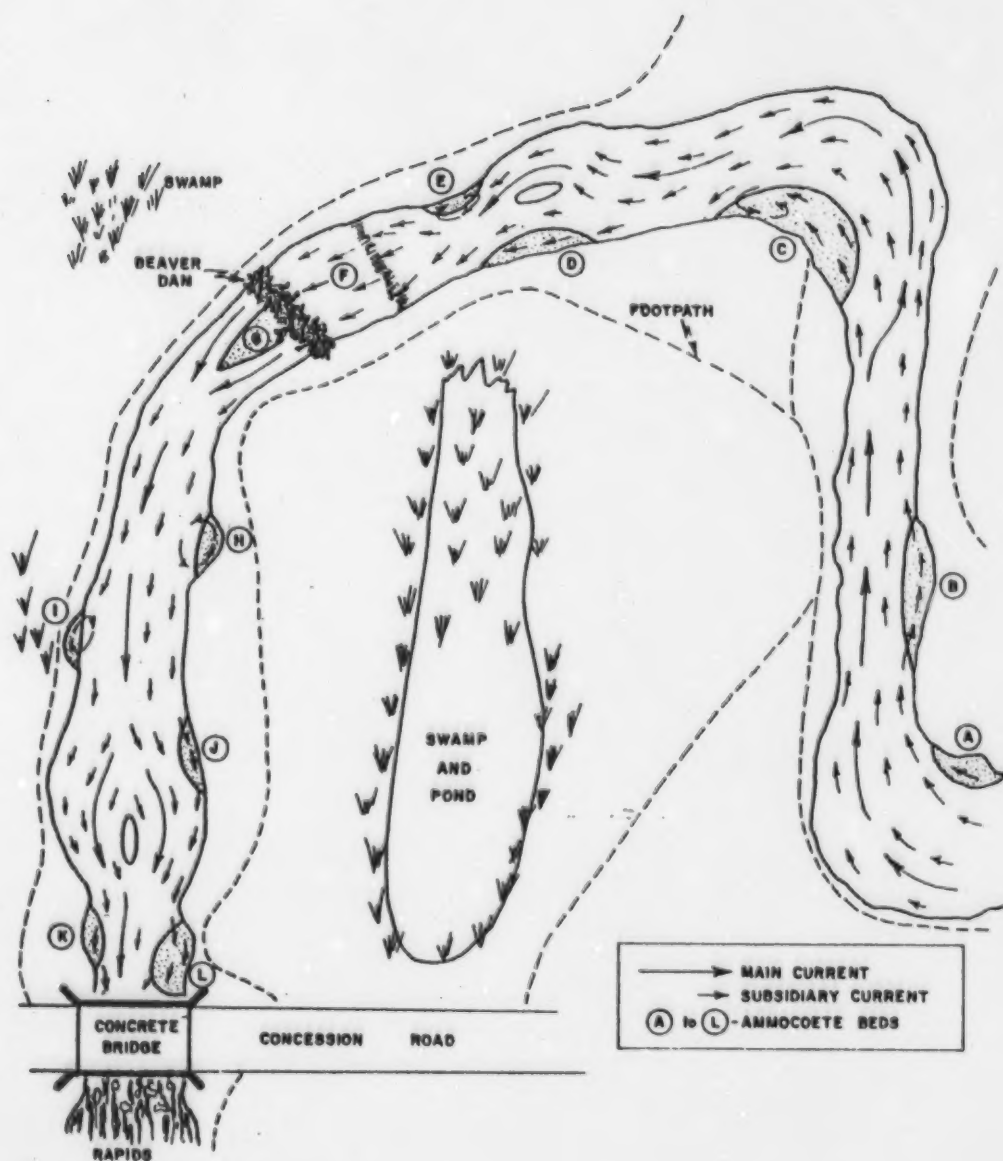


Fig. 47. Ammonoete beds in the most downstream part of the course of Venison Creek in Concession #13, N. Walsingham Township.

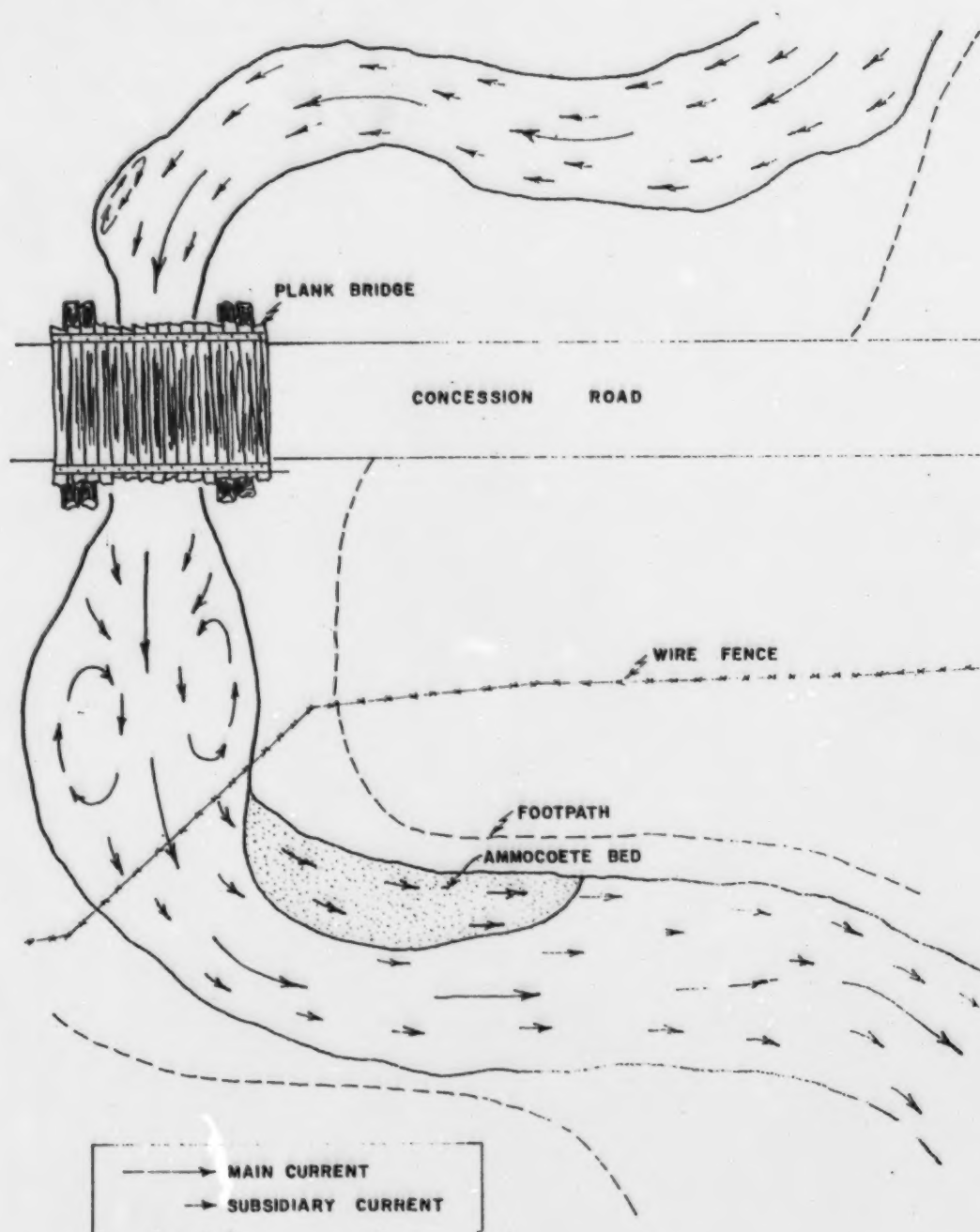


Fig. 48. Ammocoete bed in Concession #8, N. Walsingham Township, Venison Creek.

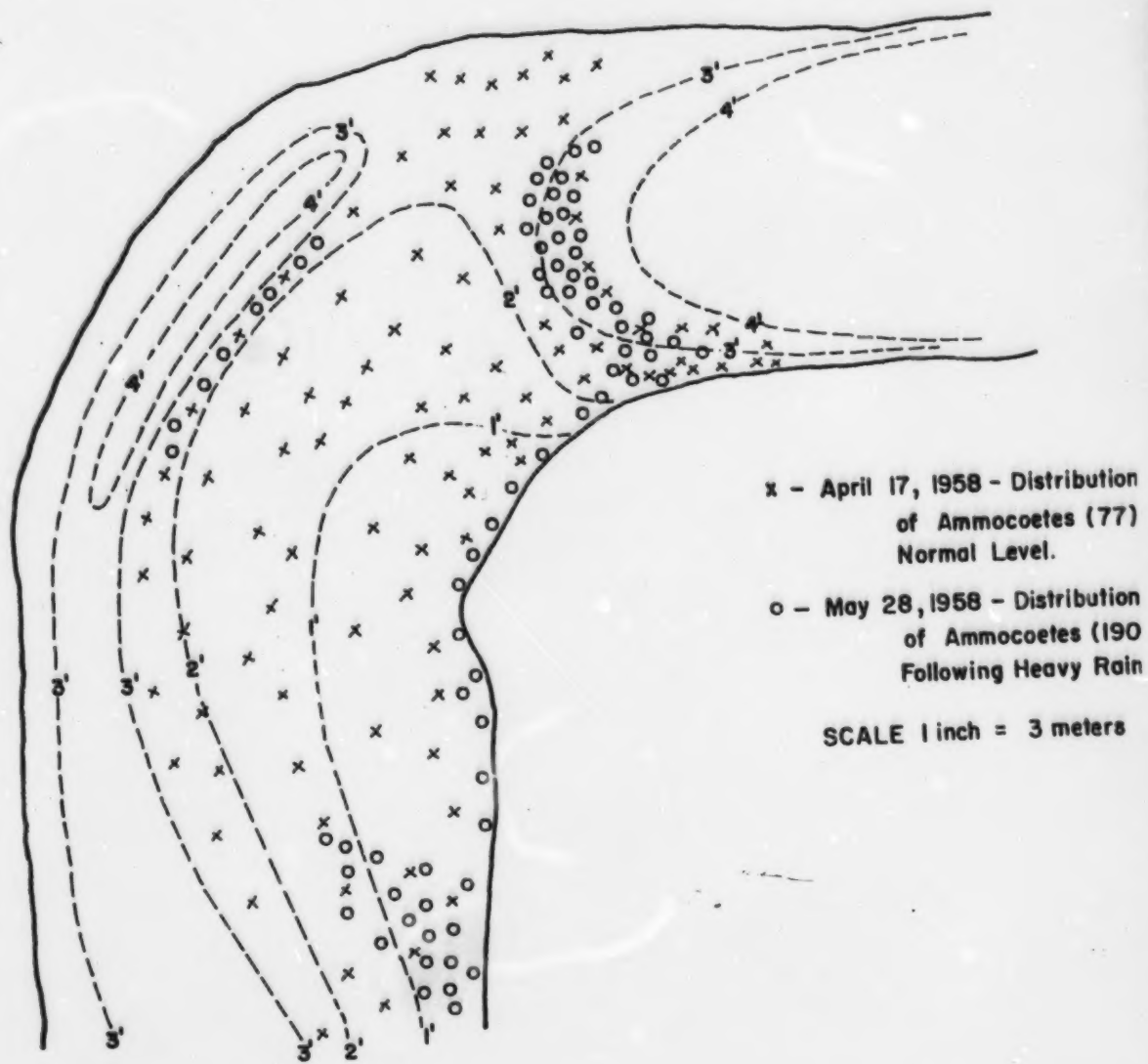


Fig. 49. Distribution of ammocoetes in the ammocoete bed at Con. #8,
 N. Walsingham Twp., Venison Creek, at normal flow and follow-
 ing heavy rain.

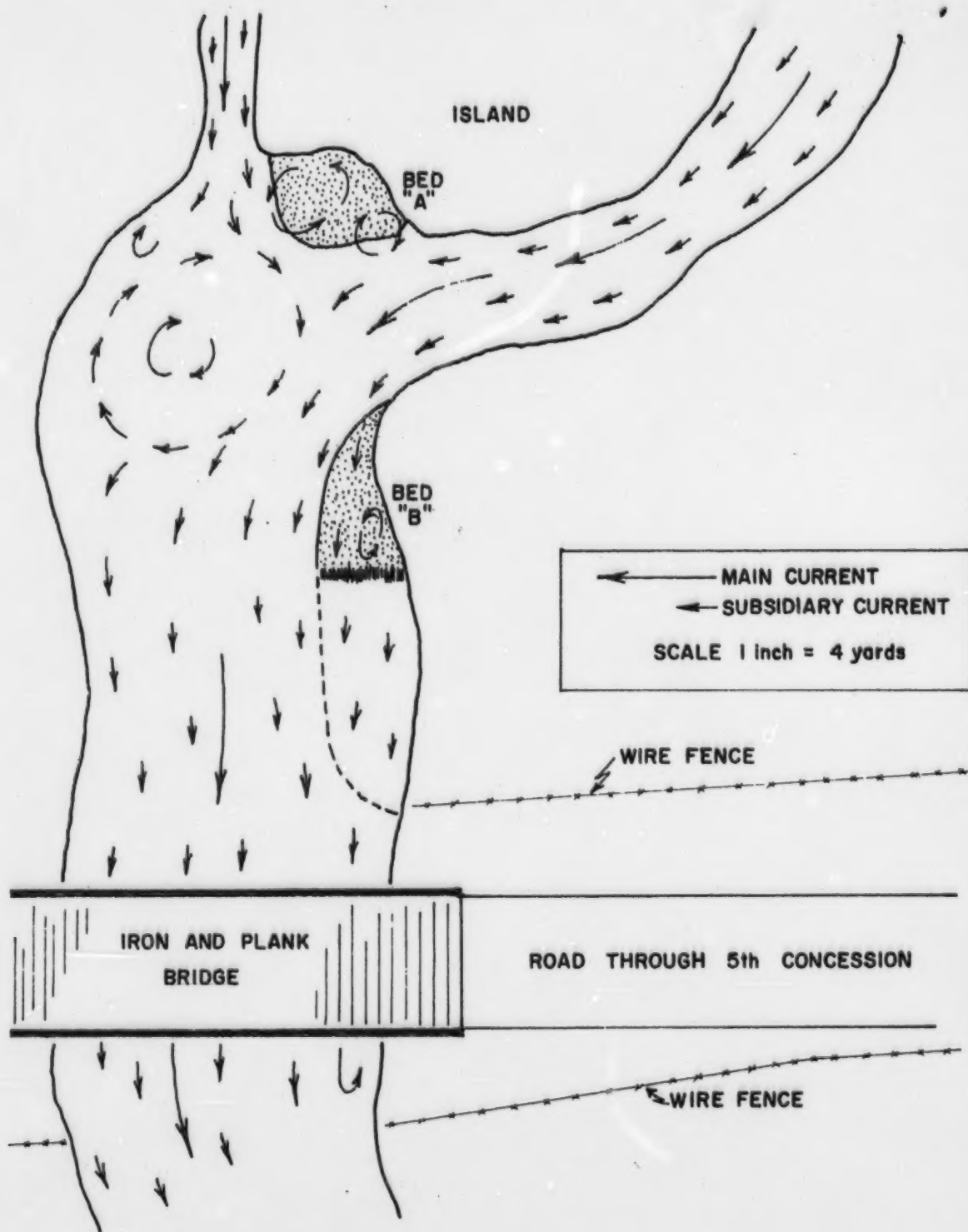


Fig. 50. Ammocoete beds in Venison Creek in Concession #5, N. Walsingham Township.

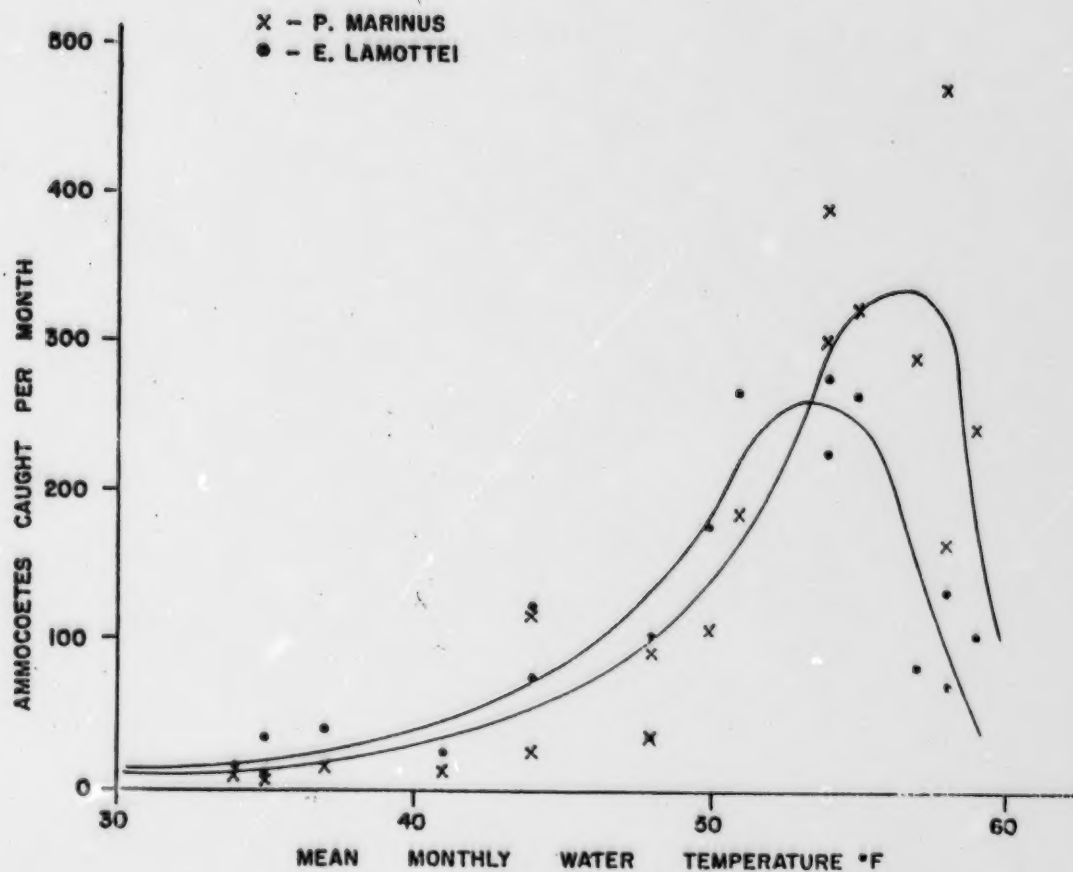


Fig. 51. Relationship between the number of ammocoetes caught at the re-shocking area in Concession #8, Venison Creek, and water temperature.